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BEHAVIOR AND SYSTEMATICS OF CEPHALOPODS FROM LIZARD ISLAND, AUSTRALIA, BASED ON COLOR AND BODY PATTERNS

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ABSTRACT

Cephalopods were observed *in situ* and under laboratory conditions at Lizard Island, Great Barrier Reef, Australia. Observations on habitat, foraging and activity patterns are included. The major chromatic components and body patterns are described for *Octopus cyanea, O. ornatus, Hapalochlaena* spp., *Metasepia pfefferi* and *Sepia papuensis*. Components of body pattern include color, texture, posture and locomotion. A remarkable new type of locomotion, "ambling," is described for *M. pfefferi*. This is the first description of living *M. pfefferi* and *S. papuensis*. On the basis of body patterns, behavior and morphology, the elevation of the subgenus *Metasepia* to generic status is confirmed. Observations of live *Hapalochlaena* at Lizard Island and in Sydney and color photographs of live animals from several other localities confirm the existence of a widespread complex consisting of at least three species and support the validity of the genus. Based on observations of live animals and a systematic evaluation of preserved specimens, the presence of *Octopus ornatus* is reported in Australian waters for the first time.

Key words: *Octopus; Sepia; Metasepia; Hapalochlaena;* cephalopods; color patterns; behavior; systematics; field observations; Great Barrier Reef.

INTRODUCTION

An International Workshop on Molluscs was conducted on Lizard Island, Australia, from 2 to 14 December, 1975 (Ponder, 1979).[3] The Workshop was sponsored by the Australian Museum, Sydney, which operates the Lizard Island Research Station located near the northern end of the Great Barrier Reef, Queensland, at 14°40′S, 145°28′E (Fig. 1). Lizard Island is a continental island about 2.9 square km in area composed primarily of granite; it lies about 30 km off the coast and is 17 km from the outermost barrier reefs (Ponder, 1979). Participants included malacologists from Australia, Great Britain, Hong Kong and the United States. One of us (C.F.E.R.) participated in the Workshop with the objective of surveying the cephalopod fauna around Lizard Island. Cephalopods were collected in various habitats and live animals were observed in their natural habitat and in aquaria. A preliminary checklist with collection and habitat data for the 27 species of cephalopods collected at Lizard Island was published separately (Roper & Hochberg, 1987).

This paper presents observations on behavior and body patterning made in the field and in laboratory aquaria on five species of cephalopods: *Octopus cyanea* Gray, 1849; *O. ornatus* Gould, 1852; *Hapalochlaena* cf. *maculosa* (Hoyle, 1883); *Metasepia pfefferi* Hoyle, 1885, and *Sepia papuensis* Hoyle, 1885. One *Hapalochlaena* cf. *fasciata* (Hoyle, 1886) was maintained in an aquarium at the Australian Museum, Sydney, subsequent to the Workshop. For the purpose of future identification, a synopsis is provided in which species characters are diagnosed and information on distributions and life histories are summarized. In addition to color and body patterning, observations are included on foraging, resource partitioning and activity patterns.

We regard these as preliminary observations that were made in 1975 in a fortuitous and opportunistic manner prior to the formulation of a classification of behavior that characterizes more recent studies of color and

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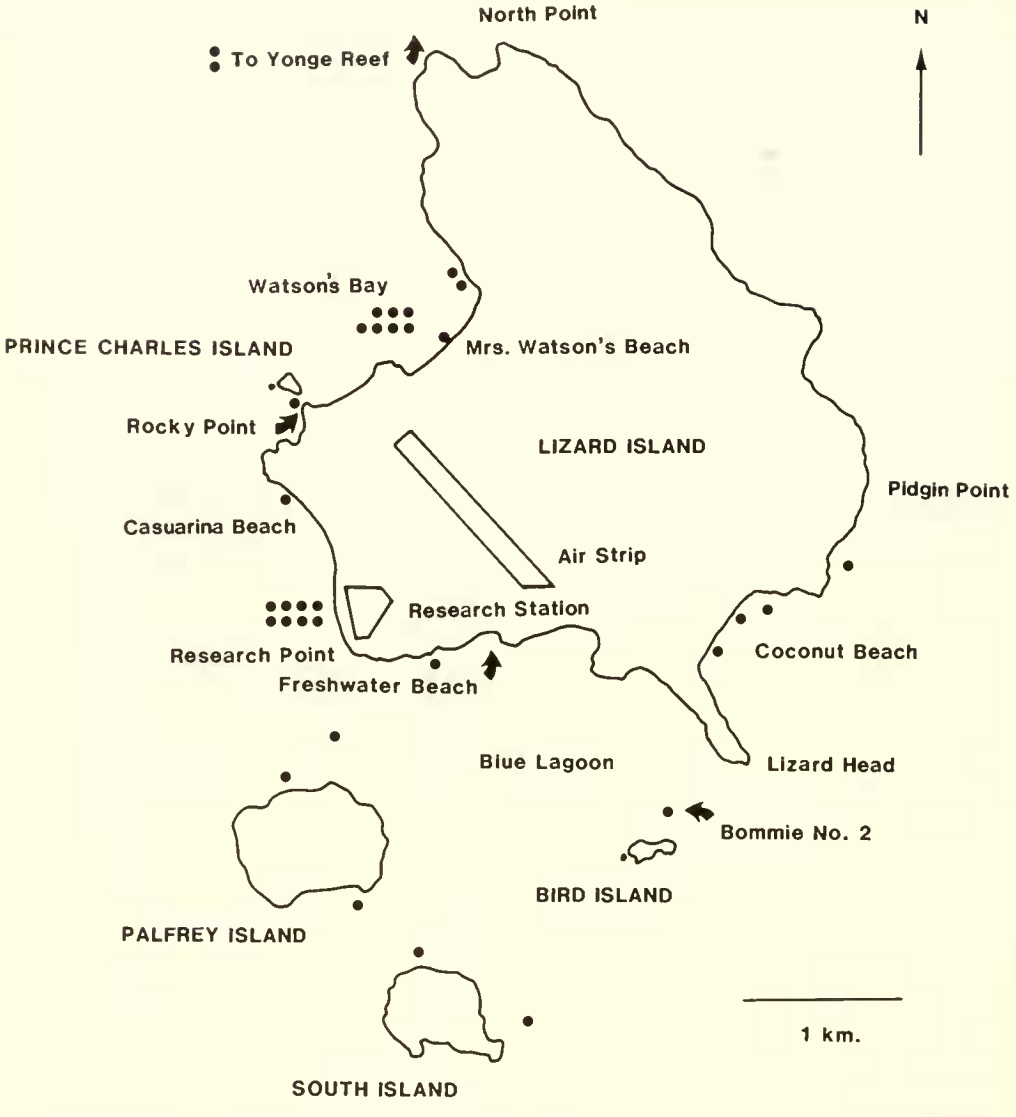


FIG. 1. Map of Lizard Island, Australia (14° 40'S, 145° 28'E) showing adjacent islands and locations of collecting stations (solid dots). See Roper & Hochberg (1987) for station and habitat data.

body patterning in squids, octopuses and cuttlefishes; see especially Holmes (1940), Packard & Sanders (1969, 1971), Moynihan (1975, 1985), Moynihan & Rodaniche (1977, 1982), Packard & Hochberg(1977), Hanlon & Hixon (1980), Boyle & Dubas (1981), Hanlon (1982), and Hanlon & Messenger (1988).

Two papers are especially significant in relation to our work. Packard & Hochberg (1977) defined and summarized the hierarchy of anatomical and behavioral systems that lead to the generation of patterns in *Octopus* and other genera. Hanlon & Messenger (1988) present a comprehensive and detailed study of body patterns and behavior in *Sepia officinalis*. To the extent possible we have attempted to follow the concepts and terminology presented in these two papers, which we consider the standards for modern work. Both papers emphasize that these magnificent and complex animals are capable of providing an almost infinite number of combi-

nations and gradations of colors, textures, postures and body patterns. Two of the genera we worked with, *Hapalochlaena* and *Metasepia*, are so different that we could not always fit our observations into existing terminology and hence have introduced several new terms.

The majority of detailed research on color and body patterning in cephalopods has been done on species from the Mediterranean and Europe, the Caribbean and Gulf of Mexico, the west coast of North America, Panama, Hawaii, Palau and Guam. Other than photographs of blue-ringed octopuses and occasionally of other octopuses and cuttlefishes that have appeared in popular magazine articles, little information is available on the biology, behavior and body patterns of Australian cephalopods.

This paper describes for the first time color and body patterns and other aspects of behavior of living *Hapalochlaena* spp., *Metasepia pfefferi* and *Sepia papuensis*. It also expands the observations made on *Octopus cyanea* and *O. ornatus* in Hawaii (e.g. van Huekelem, 1966, 1973, 1983; Wells & Wells, 1970) and on *H.* cf. *fasciatus* in Australia (e.g. Tranter & Augustine, 1973, as *H. maculosa*). In addition, we describe for the first time "ambling" in *M. pfefferi*, a newly recognized mode of locomotion for sepiid cephalopods.

MATERIALS AND METHODS

Observations and collections were made in the intertidal zone (primarily during low tides at night) and on the patch, fringing and barrier reefs by skin and SCUBA diving. Thirty-seven stations were occupied at Lizard Island for collection and observation during the Workshop. See Fig. 1 for the location of collecting sites. In the text, stations occupied by the senior author are indicated by the abbreviation CFER. For a complete list of stations and for a checklist of all cephalopods recorded from Lizard Island, see Roper & Hochberg (1987). Station data, diving logs, notes on field and laboratory observations are contained in a notebook on file at the National Museum of Natural History, Washington, D.C.

Cephalopods collected for observation were returned to the Lizard Island Research Station where they were maintained in aquaria supplied with running seawater. Glass-walled aquaria varied from 20–30 liter capacity tanks for small individuals of *Hapalochlaena* cf. *maculosa*, *Metasepia pfefferi* and *Sepia papuensis* to a large 150–200 liter tank that housed *Octopus cyanea* and *O. ornatus*. Aquaria contained fine, light-colored sand, coral rubble or other material to provide a resemblance of habitat for each species. Activity and behavior of all animals were observed both during the day and at night. Results of observations were recorded or sketched in a notebook (day) or tape recorded (night) for later transcription. Photographs, using Kodachrome 64 film, were taken with a Nikon F 35 mm camera, 55 mm macro lens and one or two Braun electronic flash units. Observations on a live *Hapalochlaena* cf. *fasciata* were made following the Workshop at the Australian Museum, Sydney. The animal was kept for two weeks in a 20 liter aquarium where it was studied and photographed.

Following observation, cephalopods were fixed in 8% buffered sea water formalin. Voucher specimens of all species discussed in this paper are deposited in the Department of Invertebrate Zoology—Mollusks, National Museum of Natural History, Washington, D.C. or in the Department of Malacology at the Australian Museum, Sydney.

The species, number of individuals and museum catalog numbers of these vouchers are: *Octopus cyanea* (2 specimens), USNM 816646 and 816647; *Octopus ornatus* (2 specimens), USNM 816649 and 816650; *Hapalochlaena* cf. *maculosa* (4 specimens), USNM 730598, 730599 and 816623; *Hapalochlaena* cf. *fasciata* (1 specimen), Australian Museum; *Metasepia pfefferi* (14 specimens), USNM 816620 and 816621; *Sepia papuensis* (2 specimens), USNM 816619.

While most of the terminology we use is adapted from other works (see especially Packard & Hochberg, 1977, Hanlon & Messenger, 1988) some terms need definition here. Chronic patterns are long-term (hours) patterns that allow an undisturbed animal to blend in with the substrate or background (crypsis or concealment). Acute patterns are short-term (only seconds or a few minutes) patterns produced in many cases in response to a disturbance. These patterns are striking or vivid in expression and typically stand out in bold contrast to the background. Acute patterns may take a number of forms, among which we define the following:

1) *passing cloud(s)*—conspicuous, pulsat-

ing flushes of dark color that pass in an amorphous front, unidirectionally across the body (see Packard & Hochberg, 1977).

2) *passing wave(s)*—distinct sequence of well-defined bands that pass like a set of wave fronts over the dorsal surface of the body. We introduce this term to distinguish this pattern from passing clouds, since the wave sets move both anteriorly and posteriorly at the same time.

3) *play(s) of color*—small flushes of dark color that can appear randomly anywhere on the body and radiate out from a point source (see van Heukelem, 1966).

4) *flash*—instantaneous expansion of chromatophores that highlights or darkens specific components of body patterns such as the ocelli, maculae of *Hapalochlaena* and mating stripes of *Octopus cyanea*. When expressed these components often appear to pulsate or flash.

5) *flush*—instantaneous expansion of chromatophores that can uniformly darken the entire body or when directed toward an interacting animal or disturbance can darken the body unilaterally or just dorsally (see Fig. 61).

6) *blanch*—instantaneous retraction of chromatophores that uniformly pales or whitens the entire body as in the deimatic (the "dymantic display" of Packard & Sanders, 1969) and mating patterns (see photographs in van Heukelem, 1970); the opposite of flush.

The above acute patterns may be single events (as in a flush or blanch) or multiple (as in passing waves or flashes).

Throughout we define continuous, unbroken lines that are oriented transversely as *bands* and those that run longitudinally as *stripes*. *Bars* are broken or interrupted bands and *streaks* are broken or interrupted stripes. *Diagonals* are short lines that are oriented at angles oblique to bars and streaks. *Maculae* are spots of dark chromatophores that surround the iridescent blue rings of *Hapalochlaena*. Unlike ocelli or eye spots in some *Octopus* species, the diameters of the maculae are not fixed but are capable of expanding or contracting.

Primary papillae are the largest and most conspicuous of the papillae on the body and often are erected for long periods of time. The distribution of primary papillae is fixed morphogenetically and can be used as a diagnostic feature at the genus level. A variety of characteristic shapes may be expressed such as simple conical, compound bifid, compound papillate ridge, flat-truncated flaps, etc. *Secondary papillae* are smaller and expressed only intermittently. They generally are all simple and conical in shape.

Cephalopods, in particular cuttlefishes, *swim* by means of fin undulations, *float* when buoyancy is controlled by the cuttlebone, *hover* when they gently pump water through the funnel and *jet* when they forcibly pump water through the funnel. Octopuses *scuttle* when they move across the bottom using their arms.

KEY TO ABBREVIATIONS

adep, anterodorsal eye papilla
admp, anterodorsal mantle papilla
ads, arm dark stripe
af, ambulatory flap
apw1, anterior passing wave, first wave
apw2, anterior passing wave, second wave
avep, anteroventral eye papilla
aws, arm white spot
dep, dorsal eye patch
dhdf, dorsal head dark field
dhws, dorsal head white spot
dhwt, dorsal head white triangle
dmdf, dorsal mantle dark field
dmds, dorsal mantle dark spot
dmlf, dorsal mantle light field
dmp, dorsal mantle papilla
dmwb, dorsal mantle white bar
dmws, dorsal mid-mantle white spot
flp, finline papilla
flws, finline white stripe
fws, frontal white spot
fwsp, frontal white spot papilla
ldmp, laterodorsal mantle papilla
lhlf, lateral head light field
lmws, lateral mantle white spot
mdmf, mid-dorsal mantle flap
mtpr, mantle tip papillate ridge
mwbf, mantle white bar flap
mwsp, mantle white spot papilla
pdep, posterodorsal eye papilla
pdmf, posterodorsal mantle flap
pdmp, posterodorsal mantle papilla
pdmpr, posterodorsal mantle papillate ridge
phws, posterior head white spot
pmds, posterior mantle dark spot
pmws, posterior mantle white spot
ppw1, posterior passing wave, first wave
ppw2, posterior passing wave, second wave
ppw3, posterior passing wave, third wave

vepr, ventral eye papillate ridge
wws, web white spot

I, dorsal arm
II and III, lateral arms
IV, ventral arm

1, primary
2, secondary

OBSERVATIONS, SYNTHESIS AND DISCUSSION

1. *Octopus cyanea* Gray, 1849.

Common name: Cyane's octopus. "Big blue octopus," the common name normally used, is a misnomer resulting from an incorrect interpretation of the specific name. Gray (1849: 15) named the species *"Cyanea,"* the capital "C" denoting a patronym referring to Cyane in Greek mythology, a nymph of Persephone who was turned into a fountain. Had Gray intended to refer to the color blue, he would have had to use the word "cyaneus," uncapitalized. Hence, the correct common name should be "Cyane's octopus." This is often called the "day octopus" in Hawaii.

A. Synopsis

Diagnosis: Body globose, muscular, mantle length to 100 mm, total length to 1200 mm, total weight to over 5 kg; skin smooth to heavily papillate, with two conspicuous web ocelli; eyes large; arms medium length, subequal, 4–5 times mantle length, thick and muscular; arm formula typically IV.I.II.III; enlarged suckers on all arms of males, especially conspicuous on arms I and II; gills with 9–10 lamellae per demibranch; right arm III hectocotylized, length 75–80% of left arm III; end organ minute, 0.5–1.5% of hectocotylized arm length; ligula bluntly pointed, open with low inrolled edge, groove with faint ridges, calamus small; eggs small, 2.5–3.0 mm long; hatchlings planktonic.

Distribution: Widespread in tropical waters of the Indo-Pacific from Hawaii through the Pacific Islands to Australia, through the Indian Ocean to East Africa and the Red Sea. One of the most common shallow-water octopuses in New South Wales and Queensland, Australia. Found in rocky or coral reef habitats from the intertidal zone to 45 m.

Life history: Reviewed in van Heukelem (1983). This large octopus is commercially important in Hawaii and elsewhere in the South Pacific.

References: Berry, 1914; Le Souef & Allen, 1933, 1937; Boone, 1938; Dew, 1959; Vevers, 1961; Young, 1962; van Heukelem, 1966, 1970, 1973, 1979, 1983; Maginniss & Wells, 1969; Wells & Wells, 1969, 1970, 1972a, b; Yarnall, 1969; Houck, 1982; and Young, Harman & Hochberg, in preparation.

B. Field observations

Two animals of *O. cyanea* were encountered during the study period; both inhabited dens in cemented coralline rock on the shallow reef flat directly offshore from the Research Station on Casuarina Beach. The reef flat habitat is described under the section on *O. ornatus*. Animal 1 was captured at night during low tide (CFER-18; refer to Roper & Hochberg (1987) for station data). It was placed in an aquarium and observed for 12 days. Animal 2 was discovered during a daytime dive on the reef flat at high tide (CFER-27). *In situ* observations on animal 2 continued for nine days.

All *in situ* observations on animal 2 were made during daytime within three hours before or after high tide. The den, located in a pile of rubble and cemented coralline rock, was elevated about 60 cm above the surrounding reef flat. The entrance was littered with a midden of mollusk shells, crustacean parts and coralline pebbles. When examined three days later the den was empty. An intense search along the contour of the reef flat revealed an occupied den about 20 m N of the first den. Although the occupant from den 1 had not been tagged and no unusual markings had been noted, the animal in den 2 was very similar in size and appearance.

On the last day of the Workshop, den 1 was still vacant. Den 2 also was empty, although a pile of fresh shells littered the front entrance. Further searching located a third den 30 m along the reef flat N of den 2. It was occupied by a large *O. cyanea* that appeared to be the same as the individual observed during the preceding week.

Octopus cyanea is a transient den dweller that moves periodically from den to den along the reef in search of food or in response to disturbance (van Heukelem, 1966, 1983). Yarnall (1969) and van Heukelem (1966) reported that *O. cyanea* may use its den for up

to one month or more. In this regard it resembles the behavior of *O. vulgaris* (Hochberg & Couch, 1971) and *O. bimaculatus* (Ambrose, 1982) (see Table 3). *Octopus cyanea* is active during morning and early evening hours and remains quiescent in its den during the day and at night (Houck, 1982). Loch (1980) discussed the hole-drilling technique used possibly by *O. cyanea* to feed on three species of *Cypraea*. Mating, egg laying and brooding have been reported by van Heukelem (1970, 1983) and Le Souef & Allan (1933, 1937).

Although a large number of dives was made by the Workshop participants in the reef flat area adjacent to the Research Station, only two *O. cyanea* were observed. In contrast, over 30 individuals of *O. ornatus* were observed in the same area during only three excursions onto the reef flat at night during low tide. *O. ornatus*, like *O. macropus*, apparently is a more free-ranging species that is active at night (van Heukelem, 1966; Houck, 1982) (see Table 3).

C. Components of body patterns

Octopus cyanea is a robust, medium-sized species similar to *O. vulgaris* or *O. bimaculatus*. The body is heavy set and the arms relatively short and muscular. When occupying its den, *O. cyanea* assumes one of two body postures that we term the "lookout" (Figs. 2–4) and the "guard" (Fig. 5) postures. In the lookout position the head and eyes are raised out of the entrance of the den with the eyes greatly protruded, so the animal can monitor activities around the den (Figs. 2–4). In this posture mantle, head, web and arms are covered densely with both flat-truncate and conical, cream-colored papillae that give the animal a very rugose appearance that blends well with the surrounding habitat. A single, large compound papilla generally is erected over each eye (Figs. 2, 3); three or four additional simple dorsal eye papillae also may be present. The entire body is covered with a light mottle of reddish purple/maroon on a beige/cream background. Two large ovate ocelli ("eye spots") often are visible on the web just below (anteroventral to) the eyes (Fig. 31). The aboral and lateral surfaces of the arms are banded with dark patches of red interrupted by small to medium-sized white spots. The papillate skin and coloration match the irregularly textured and mottled appearance of the substrate. When approached closely or disturbed the animal abandons the lookout posture, flushes a dark mottled maroon/red with alternating dark maroon and cream lines or rays radiating around the eyes (Fig. 5) and then retreats into the den.

In the "guard" posture the octopus is withdrawn into the den and sits sideways just inside the entrance. The eye (either right or left) is erect and peers out over the second and third arms that are extended across the entrance and turned outward so that the largest suckers are exposed and visible (see Fig. 5). In this position the octopus can effectively guard the entrance visually; it also can grasp and test with the exposed suckers anything that approaches the entrance to the den. In the guard position the entire animal is covered with primary cream-colored papillae, both simple, conical as well as flat-truncate papillae. The primary papilla over each eye is leafy and flat and may bear three or four secondary papillae (Fig. 2); primary compound papillae also occur anterior to the eyes, in the mid-line at the junction of the web and head, and one each at the base of the arms. Typical cryptic coloration is a light mottle of red/brown on a cream/beige background. A dark black band extends along the head and through the eye effectively masking it. When disturbed the animal flushes a dark mottle and the eye mask changes to the radiating pattern of light cream and dark red lines mentioned above. Upon repeated disturbance the animal flushes a uniform dark red. The dark flush starts at the head and radiates down the arms and mantle until the animal is a uniform dark color.

When seen in the open or when disturbed enough to leave the den, the animal jets across the bottom. When jetting, the body texture is smooth to granular without conspicuously erect papillae, and the color is light cream mottled with red patches (Fig. 6).

When approached in the aquarium by *O. ornatus*, the captive *O. cyanea* exhibited a typical response in which the body reared up and the arms flared out to present the enlarged suckers. This is equivalent to the "fighting display" of Packard & Sanders (1971). The animal changed from a cryptic color pattern to a uniform dark flush. Such posturing effectively drove off the *O. ornatus*.

An inventory of the currently recognized components exhibited by *O. cyanea* is presented in Table 1. The data are based on our observations of live animals at Lizard Island and on published reports, figures and photographs.

FIGS. 2–5. *Octopus cyanea*. Figs. 2, 3: Frontal view (2) and left lateral view (3); lookout posture with raised flat, truncate dorsal eye papillae. Fig. 4. Frontal/lateral view, left side; lookout posture without raised papillae. Fig. 5. Left lateral view; guard posture with radiating dark and light lines around eye, and exposed suckers. Photographs by W. F. van Heukelem (Honolulu, Hawaii).

FIG. 6. *Octopus cyanea*. Right lateral view, jetting in forward direction over the bottom in light color phase without erect papillae. Photograph by W. F. van Heukelem (Honolulu, Hawaii).

D. Discussion

The observations on *O. cyanea* at Lizard Island basically confirm those of other workers (especially van Heukelem, 1966, 1983) in that the species is active during crepuscular periods and quiescent during both night and day. A widely-spaced, transient den-dweller, *O. cyanea* on Lizard Island ranges along the reef flat, occupying one den for a few days to several weeks before moving on to the next. Niche and food resource partitioning are discussed in the following section on *O. ornatus*.

Van Heukelem (1983) stressed that *O. cyanea* is capable of showing a large variety of color patterns, textures and postures but that a detailed inventory had not been formulated. Illustrations and brief notes on color and body patterns are in the literature: sexually mature adults (van Heukelem, 1966, 1983; Wells & Wells, 1972b), brooding females (Le Souef & Allan, 1933, 1937), hatchlings (Le Souef & Allan, 1937; Dew, 1959) and newly settled juveniles (Wells & Wells, 1970). Hawaiian specimens of *O. cyanea* were described and figured by Hoyle (1885a, 1886, see also Berry, 1914) under the name *O. marmoratus,* which refers to the color pattern of "ochreous red maculated with purple" and to the series of "intercotyledonary color bands down the surface of the arms."

Taki (1964) provided additional notes on color of a species he described as *Callistoctopus magnocellatus* but this is now known to be a synonym of *O. cyanea.* Taki's species name refers to the presence of a large ocellus that he described as having three parts: a black center 22 mm in diameter, a pale ring and an outer black ring 3–4 mm wide. The total diameter measured 40 mm. In other octopuses the ocellus also is known to contain species specific patterns of chromatophores and iridophores (Hochberg, in preparation); this character needs further detailed documentation.

The best records of the color and patterns of this species are photographs such as those in van Heukelem (1970, 1983), Voss (1971), Roessler (1977) and Travieso (1978). Of all the patterns of *O. cyanea*, perhaps the most colorful and interesting are the dramatic courtship and mating patterns. Although not

observed at Lizard Island these have been photographed and well documented in Hawaii by van Heukelem (1966, 1970, 1983) and by Wells & Wells (1972b).

To prepare a complete inventory of patterns in *O. cyanea*, extensive field and laboratory observations of young and adult animals are needed. In addition, further comparisons of patterns need to be made in widely separated geographic populations.

2. *Octopus ornatus* Gould, 1852.

Common name: white striped octopus. This common name is used to emphasize the pattern of conspicuous white markings on the mantle. This is often called the "night octopus" in Hawaii.

A. Synopsis

Diagnosis: Mantle globular to elongate, muscular, mantle length to 120 mm, total length to 1000 mm, total weight to 500 g; skin granular to rough and warty, purplish red, with conspicuous pattern of white markings on the mantle and elongate oval or round white spots on arms; eyes large; arms very long, attenuate at tips, thick and muscular proximally, 6–8 times mantle length; arm formula I.II.III.IV; enlarged suckers on arms I of males; gills with 12–14 lamellae per demibranch; right arm III hectocotylized, length 60–75% of left arm III; end organ medium sized, 4.5–8% of hectocotylized arm length; ligula elongate, pointed, inrolled edges, groove smooth to faintly striated, calamus small; eggs small, 2–4 mm long; hatchlings planktonic.

Distribution: Widely distributed in tropical waters; Indo-Pacific from Hawaii through the Pacific islands to Australia, into the Indian Ocean to East Africa; common shallow water species, free ranging through reef flat areas, from intertidal to 15 m. This is the first confirmed report of the species in Australia. Known currently only from the Great Barrier Reef, northern Queensland.

Life history: Life span not known. Large numbers of small eggs are laid. Larvae are planktonic upon hatching. Feeds principally on small crustaceans. Active at night. Free ranging predator, without fixed dens.

References: Gould, 1852; Berry, 1914; Boone, 1938; Taki, 1964; van Heukelem, 1966; Yarnall, 1969; Voss, 1981; Houck, 1982; and Young, Harman & Hochberg, in preparation.

B. Field observations

Thirty individuals of *O. ornatus* were found in a 20 × 100 m area of the reef flat immediately offshore from Casuarina Beach and were observed during three low tide surveys conducted on the reef on moonless nights.

At low tide much of the reef flat was exposed leaving a network of tide pools that varied in size from small shallow puddles to pools several meters across with depths to 15–20 cm. The bottom of the tide pools consisted of coarse coralline sand and small pieces of coral rubble. The reef flat habitat consisted of scattered heads of dead coral, coralline algae and rubble, and it appeared to be ideal for *O. ornatus*. The many holes and crevices provided numerous places of protection for resting octopuses, as well as refuge for prey animals, particularly crabs.

Three individuals were observed scuttling over open sandy bottom immediately shoreward of the reef flat, but all others were associated closely with the reef flat pools. One individual hunted by scuttling slowly over the reef flat while the long, sinuous arms were engaged simultaneously in search of prey. The arms were fanned out in all directions, exploring every nook and crevice in the pool. Several arms investigated deep into holes, while others swept under rocks. During the observation period this individual captured two small crabs (unidentified) that immediately were transferred to the web and later devoured.

Although frequent dives were made in the reef flat area during the 12-day period of the Workshop, *O. ornatus* never was observed during the daytime, nor were any found at rest in dens. We assume the animals either hide deep in the reef complex or bury themselves in the sand where they remain quiescent all day. This is in sharp contrast to *O. cyanea*, a crepuscular den dweller, and is similar to the behavior of *O. macropus* (Hochberg & Couch, 1971) (see Table 3).

C. Components of body patterns.

The mantle of *O. ornatus* is elongate and pointed posteriorly. The arms are extremely long, slender and attenuate. The typical cryptic body pattern in the field is a low-intensity, light, brownish-red mottle. The mantle, head, web and arms are covered with light cream to white colored markings (Fig. 31), the vividness of which is controlled by overlying dark

TABLE 1. The components of body patterns in *Octopus cyanea*.

I. Chromatic components		
A. Light	B. Dark	C. Other
arm white spots[2]	dark arm bands	ocelli
dorsal head white stripe	dark arm stripes[1]	
dorsal mantle white stripe[2]	dark arm tips[1]	
white mantle (blanch)[1]	dark uniform mantle[1]	
white web (blanch)	dark anterodorsal mantle patch[1]	
light mantle bands	dark head[1]	
	dark eye stripe	
	dark eye region[1]	
	radiating eye lines	
II. Textural components		
A. Primary papillae	B. Secondary papillae	C. Other
(compound, flat)	(simple, conical)	granular
dorsal eye papillae (1/eye)	dorsal eye papillae (3 or 4/eye)	smooth
mantle papillae	uniform body papillae	
arm base papillae (1/arm)		
III. Postural components		
radiating arms	standing[1]	
curled arms	lookout (= alert[1])	
coned arms	guard	
flared arms	submissive:	
raised head & eyes	male/male[1]	
enlarged sucker presentation	male/female[1]	
sucker shield[1]	flared web	
IV. Locomotor components and maneuvers		
sleeping	prey drilling	
resting/sitting	inking	
scuttling	ritualized fighting[1] (= territorial defense)	
jetting	distance copulation[1,4]	
escape (body first)	courtship strut[1]	
stalking (arms first)[1]	bobbing[1]	
hunting/prey capture	escape (body first)	
speculative pounce[1,3]	grooming[1]	
attack jump	burying	
food gathering under web		
V. Body patterns		
A. Chronic	B. Acute	
light cryptic mottle (grey, light brown)	dark conflict mottle	
light uniform	dark uniform (red or brown flush)	
sleeping[1]	light uniform (blanch):	
	deimatic (white w/ocelli[1])	
	copulatory (white w/o ocelli[1])	
	courtship stripes (male)[1,4]	
	dominant male mantle stripes[1]	
	flamboyant[1]	
	plays of color[1]	

[1]Van Heukelem (1966, 1970, 1983)
[2]Roessler (1977)
[3]Yarnall (1969)
[4]Wells & Wells (1972b)

TABLE 2. The components of body patterns in *Octopus ornatus*.

I. Chromatic components		
A. Light	B. Dark	C. Other
dorsal mantle white stripes or streaks	dark uniform	bluish-green iridescence
dorsal mantle white spots		
head white spots		
frontal white spots		
arm white spots (2 rows/arm)		
II. Textural components		
A. Primary papillae	B. Secondary papillae	C. Other
compound bifid mantle tip papillae	Simple uniform body papillae	granular
simple lateral mantle tip papillae		smooth
compound bifid dorsal eye papillae (1 or 2)		
simple frontal white spot papillae (1/white spot)		
simple arm base papillae (1/arm)		
III. Postural components		
radiating arms		
coned arms		
elongate pointed mantle		
IV. Locomotor components and maneuvers		
resting/sitting		
scuttling		
jetting		
inking		
hunting w/arms		
V. Body patterns		
A. Chronic	B. Acute	
light cryptic mottle	dark conflict mottle	
	dark uniform (flush)	
	dermatic	

chromatophores. White spots on the arms are squarish with rounded corners and arranged in two regular rows; they decrease in size to the tips of the arms. Spots on the web and head are oval and they become elongate interrupted stripes or streaks on the mantle. When a light is shone on the animal at night the white spots, stripes and light patches on the lateral surfaces of the suckers and the circumference of the suckers are visible as a vivid bluish-green iridescence (see comments by Roper & Young in Voss, 1981: 533). Body patterns observed in the field appeared identical to those seen in the aquaria and are described below. All laboratory observations were on animals captured at CFER stations 18 and 20.

During the night, inactive or resting animals sit in the typical octopus posture with the head and mantle lying horizontally over the relaxed, radiating arms and web. The mantle is finely granular, while the head and arms are smooth. The posterior tip of the mantle has several papillae. A large, bifid papilla is erect at the very tip of the mantle during jetting, while the rest of the body is smooth. Two or three simple, secondary papillae occur along each side of the lateral tip of the mantle. Above each eye is one or two low, broad, bifid papillae. A papilla also is present anterior to the eyes in the center of each white spot on the web at the base of each arm. Resting animals have a light to medium dark cryptic mottle with large subdued white spots on the head, web and arms. White markings are not visible on the dorsal mantle. When disturbed

TABLE 3. Comparison of factors for coexistence of *Octopus cyanea* and *O. ornatus*.

Factor/species	*O. cyanea*	*O. ornatus*
Body form	medium sized, robust	small, sleek
Arms	robust, normal length	very long, attenuate
Activity period	crepuscular, dawn and dusk	nocturnal
Dwelling	"territorial" in fixed den sites, periodic transient	temporary shelters, changed daily, "non-territorial"
Hunting sites	in immediate home range	over broad range
Prey	mollusks (secondarily crabs)	crabs
Mode of life	reclusive, solitary	nomadic
Relative abundance	low	high
Comparable species in other areas	*O. vulgaris* (Mediterranean, Caribbean) *O. bimaculatus* (California, Mexico)	*O. macropus* (Mediterranean, Caribbean) *O. alecto* (Mexico)

the animal first darkens the mottle and then produces a uniform dark flush that covers the entire body.

All arms are engaged in locomotion when the animal scuttles rapidly across the bottom at night. During this type of locomotion the mantle is elongate and pointed posteriorly. The entire body is smooth except in the posterior region where several primary papillae are erect. The animal shows a darkened mottle in which the white markings are visible.

While the animal is at rest during daytime, the coloration is a deep brownish red reticulation with subdued white markings. Occasionally three small white spots may show on the dorsal mantle, one in the midline just posterior to the junction of the mantle and head and two (the dorsal mantle white spots) lateral to the midline and in the anterior third of the mantle.

When disturbed, *O. ornatus* jets mantle-end first across the bottom. The mantle is elongate and pointed and the arms are brought together in a cone. The body is streamlined with the skin entirely smooth except for the above-described primary papillae erected on the posterior tip of the mantle. Color is a light to dark mottle to nearly uniform dark with vivid white markings.

Table 2 presents the currently recognized components of body patterns of *O. ornatus* based upon our observations and a compilation from published reports and photographs.

D. Discussion

Octopus ornatus has been studied primarily in Hawaii (van Heukelem, 1966; Houck, 1982). The Lizard Island animals represent the first records of this species in Australian waters, and our observations confirm those made in Hawaii. On Lizard Island, animals are conspicuously abundant at night as they range across the reef flats actively hunting cryptic prey, primarily crabs, with very long, attenuate arms. During the day the animals retreat to temporary shelters of convenience, rather than to any permanent den site, or they may burrow into the sand.

The observations on *O. ornatus* and *O. cyanea* living sympatrically on a small area of patch reef suggest a system of niche and food resource partitioning. Table 3 presents the currently recognized morphological and ecological characteristics that permit these two species to coexist in the same habitat. The existence of ecomorphs has been demonstrated in other groups. We suggest that this phenomenon occurs between *O. cyanea* and *O. ornatus* and may occur in a number of sympatric octopod species in various parts of the world.

Little information is available on the color, texture and body patterns of *O. ornatus.* A color plate by J. Drayton appeared in the original description by Gould (1852) along with notes on the color of the living animal. Taki (1964) illustrated his description of *Callistoctopus asakawai* (now regarded as a synonym of *O. ornatus*—see Voss, 1981) with a color painting of a preserved specimen and several black and white photographs of live animals. Additional brief references to color and texture are noted in Berry (1914), Boone (1938), van Heukelem (1966) and Voss (1981). The majority of these papers concentrate on the striking pattern of white spots or stripes but do not provide other color or pattern observations. Van Heukelem (personal communication) reported differences in

basic ground color (from deep orange to dark purplish brown to deep reddish brown) that appear to have a geographic or populational basis. This may be an artifact of observation and preservation or an indication that a complex of cryptic species may be involved.

Van Heukelem's photograph (1970) of *O. ornatus* in Hawaii is reproduced here (Fig. 31) for reference to the conspicuous pattern of white markings of this species. *O. ornatus* closely resembles *O. macropus* (see Hanlon, this volume, for comparison photograph), a species that has white spots instead of stripes on the mantle. *O. macropus* has been reported in Australia (Lu & Phillips, 1985). Careful study and comparison of *O. ornatus* and *O. macropus* should be made, since in many parts of the world their distributions appear to overlap.

3. *Hapalochlaena* cf. *maculosa* (Hoyle, 1883)

Common name: Lesser blue-ringed octopus. We introduce this name to draw attention to the very small blue rings (1–2 mm in diameter) on the mantle, head, web and arms.

A. Synopsis

Diagnosis: Mantle small, elongate, ovoid, pointed posteriorly; mantle length to 30 mm; total length to 80 mm; total weight to 40 g; skin wrinkled or densely covered with papillae, with conspicuous pattern of dark maculae and small iridescent blue rings (1–2 mm in diameter) on dorsal mantle, head, web, and arms, ventral head and mantle without rings; eyes large and prominent; arms short, subequal, 1.5 to 2 times mantle length; typical arm formula III.II = IV.I; suckers small, numerous, none enlarged; gills with 6 or 7 lamellae per demibranch; right arm III hectocotylized, length 70 to 80% of left arm III; end organ medium size, 4 to 6% of hectocotylized arm length; ligula smooth; calamus small; egg size unknown.

Distribution: This species appears to be widespread, perhaps as a complex of species, all around Queensland, Victoria, Tasmania, South Australia and Western Australia. In tropical waters it occurs close to coral reefs in shallow water to 25 m, on sandy silt bottom, apparently in association with attached green algae. In temperate waters it occurs in rock reefs and rock rubble areas, tide pools, mollusk shells, bottles and cans.

Life history: Unknown.

References: See *H.* cf. *fasciata*.

B. Field observations

Four individuals of *Hapalochlaena* cf. *maculosa* were collected during the day in Mrs. Watson's Bay. Animal 1 was discovered in 14 m (CFER-25) and animal 2 in 20–22 m (CFER-28). Both were found on open sand/silt bottom devoid of rocks but scattered with coral rubble and living solitary corals. Conspicuous fauna and flora included numerous black holothurians, probably *Holothuria atra* or *H. edulis*, scattered patches of attached green algae, *Caulerpa cupressoides* and *Halimeda* sp. When first sighted, animal 1 looked like a piece of alga.

Animals 3 and 4 were captured at 12 m (CFER-42) on a mixed sand and silt bottom dominated by a dense stand of *Halimeda* sp., scattered *Caulerpa cupressoides*, many large black holothurians and a few brown-yellow holothurians (probably species of *Holothuria*, *Pentacta* or *Stichopus*). Both animals were observed in close association with *Halimeda* plants. Animal 3 was clinging with the tips of its outstretched arms to the upright branches of the alga about 3 cm above the bottom. The skin showed cryptic coloration of mottled olive-green/brown and was finely papillate; this patterning very closely matched the color and texture of the *Halimeda*. No spots or blue rings were evident. When capture was attempted with a small net, the animal escaped and flashed a vivid pattern of dark patches (maculae) surrounding bright, iridescent blue rings. The animal immediately dropped to the bottom and resumed a pale cryptic pattern to match the grey/beige color of the substrate. All rings and patches disappeared. When finally captured, it again flashed its dark chromatophore patches and iridescent blue rings. This behavior also was elicited in the aquarium and is described in detail below.

When animal 4 was first approached by the diver, it was hovering in a motionless position immediately above a *Halimeda* plant. The animal was oriented with the body at a 45° angle to the bottom and the arms drooping downward. A cryptic color pattern and papillate texture covered the entire body. When the diver was sighted the animal instantly dropped to the bottom, as if in a "free fall," and assumed the characteristic deimatic pat-

tern with arms spread out, web expanded and a pale color. Upon capture the animal flashed its vivid blue rings and surrounding dark maculae, then flushed dark reddish brown.

The *Halimeda* plant to which animal 3 was clinging was inhabited by a rich fauna of epiphytes that included small gastropods, scallops and other bivalves, a small stomatopod and several hermit crabs and swimming crabs. This would seem a rich source of food for a small octopus like *Hapalochlaena*. In the laboratory the animals were maintained on small *Ocypode* crabs. *Hapalochlaena* cf. *maculosa* also has been observed clinging to *Caulerpa cupressoides,* another green alga that provides habitat for a diversity of epiphytic organisms, including the gastropods *Engina* and *Anachis* visible in Fig. 14.

C. Components of body patterns

The Lizard Island *Hapalochlaena* have a distinct and fixed pattern of small rings 1–2 mm in diameter (Figs. 7, 8) that differ from the rings and lines of the other species. In *H. lunulata* they are fewer in number and larger, 7–8 mm in diameter (Fig. 13), whereas in *H.* cf. *fasciata* the mantle has a pattern of blue lines (streaks and diagonals) instead of rings (Figs. 11, 12). The configuration, dimensions and distribution of these characters often are obscured or distorted in preserved specimens, but they are very distinct and prominent in living animals when they are disturbed.

The ring macula complex is similar in appearance and function to the ocelli of 2-spotted octopuses such as *O. bimaculoides* (see Packard & Hochberg, 1977). The center and periphery of each ring are raised and densely invested with dark chromatophores. In the region of the ring itself, the skin overlying the blue iridophores is transparent or translucent and indented. When *Hapalochlaena* cf. *maculosa* is resting, a cryptic mottle pattern is assumed. In this pattern the blue rings essentially are invisible and the dark maculae are subdued to invisible (Fig. 18). As the chromatophores are expanded and the maculae darken, the vividness of the blue rings intensifies in a fashion similar to the expression of the blue rings in ocelli (Figs. 16, 17, 26–28). When the chromatophores are partially expanded the centers of the rings are lighter than the maculae surrounding the rings, but when the chromatophores are maximally expanded over the entire body, the centers are very dark and the blue rings may be obscured (Fig. 15). A single, small, conical papilla often is erected in the center of each ring.

During the day when the animals are inactive and resting on a sandy bottom in the aquarium the eyes are erect. The arms either are held straight out with the tips curled aborally, or they are curled and tucked up under the body. Often the animal sits partially buried in the sandy substrate. Small conical papillae are erected over the entire body. Four large, primary, light-colored, conical papillae are present on the dorsal mantle and two large compound papillae are located on the head above the eyes. A prominent light-colored, papillate ridge is located ventral to each eye. A large, flat, papillate ridge is located in the midline on the posterior dorsal mantle. The posterior tip of the mantle often is drawn out into a point with an elongate, flat, papillate ridge (Figs. 8, 9).

Resting, inactive animals all exhibit cryptic color patterns that match the background. The body and arms are either uniform light beige or a beige mottled with light brown that corresponds to the mantle and arm maculae. The iridescent blue rings are only faintly visible on the mantle, but they are slightly more conspicuous on the arms. A broad light beige stripe, the dorsal mantle light stripe, extends along the dorsal midline from the head to the posterior tip of the mantle (Fig. 15). In the mid-region of the dorsal mantle there are two conspicuous, irregularly shaped, white spots at the center of which is a single, large, mantle papilla (Figs. 7, 8, 16). A third white spot is present on the posterior mantle midline. A posterior head white spot is present on the head just posterior to the eyes. In this species it is in the shape of a curved bar or crescent. A frontal white spot is located on the head just anterior to the eyes, and a single conical papilla is present in the center of this spot. All five white spot regions appear to be underlain by dense patches of leucophores (see Figs. 7, 8, 16).

At night *Hapalochlaena* cf. *maculosa* rests with the arms curled under the body. The skin texture is granular to minutely papillate and the color a darker or more intense mottle. The frontal white spot is especially conspicuous at night in the beam of a flashlight.

Animals in aquaria were observed in a few instances to bury themselves partially in

the sand. Burying behavior is initiated as the ventral arms push sand aside laterally. As the excavation continues, arms III help to enlarge and deepen the depression. Jets of water from the funnel are not used. Only the ventral half of the mantle, head and arms III and IV are buried. The skin is uniformly papillate and the color is a light cryptic mottle that matches the substrate perfectly. This behavior was not observed in the field; however, field observations were quite limited.

Occasionally animals jet about the aquarium without being stimulated by the observer. The body is smooth except for the large, primary, mantle papillae, which are erect. The color is a uniform pale beige, and maculae and rings are not visible. In contrast, animals that are disturbed jet away in an escape reaction; the body is entirely smooth with papillae retracted. When animals are disturbed the color flushes from an intense yellowish beige mottled with dusky brown maculae to a very dark mottle. Next, the dark maculae enlarge and coalesce, coloring the octopus a uniform dark reddish brown. Often ripples of color, in the form of "passing clouds" move over the body surface. A dark stripe extends along each side of the mantle and head and through the eye, then tapers along the lateral edge of the dorsal arms nearly to the tips (Figs. 9, 10). The other arms are an intense yellow. The blue rings and associated dark maculae pulsate in synchrony, which gives the appearance of flashing rings. Ring/macula flashes initially are directed unilaterally toward a disturbance (Fig. 26). If the disturbance continues, the ring/macula flashing pattern becomes bilateral as it darkens and intensifies, then spreads wave-like over the entire dorsal and lateral surfaces of the mantle, head, web and arms (Fig. 27).

When a disturbance persists or is very intense, young *Hapalochlaena* cf. *maculosa* discharge a cloud of thin, reddish brown ink. The ink rapidly dissipates and does not congeal or "hang" in the water as a pseudomorph, as is typical in other *Octopus* species. Up to 10 clouds of ink were discharged during a period of repeated disturbances. The ink sac degenerates with growth, so that full-grown adults lack the ability to produce ink.

Table 4 presents the currently recognized components of body patterns of *H.* cf. *maculosa* based on observations and photographs at Lizard Island.

D. Discussion

A discussion of *Hapalochlaena* species appears at the end of the section on *H. lunulata*.

4. *Hapalochlaena* cf. *fasciata* (Hoyle, 1886)

Common name: Blue-lined octopus. We introduce this name to draw attention to the distinct blue lines on the mantle of this species. Because of taxonomic confusion, this species frequently has been called the "blue-ringed octopus," but we recommend that use of this common name be restricted henceforth to the true "ringed" species.

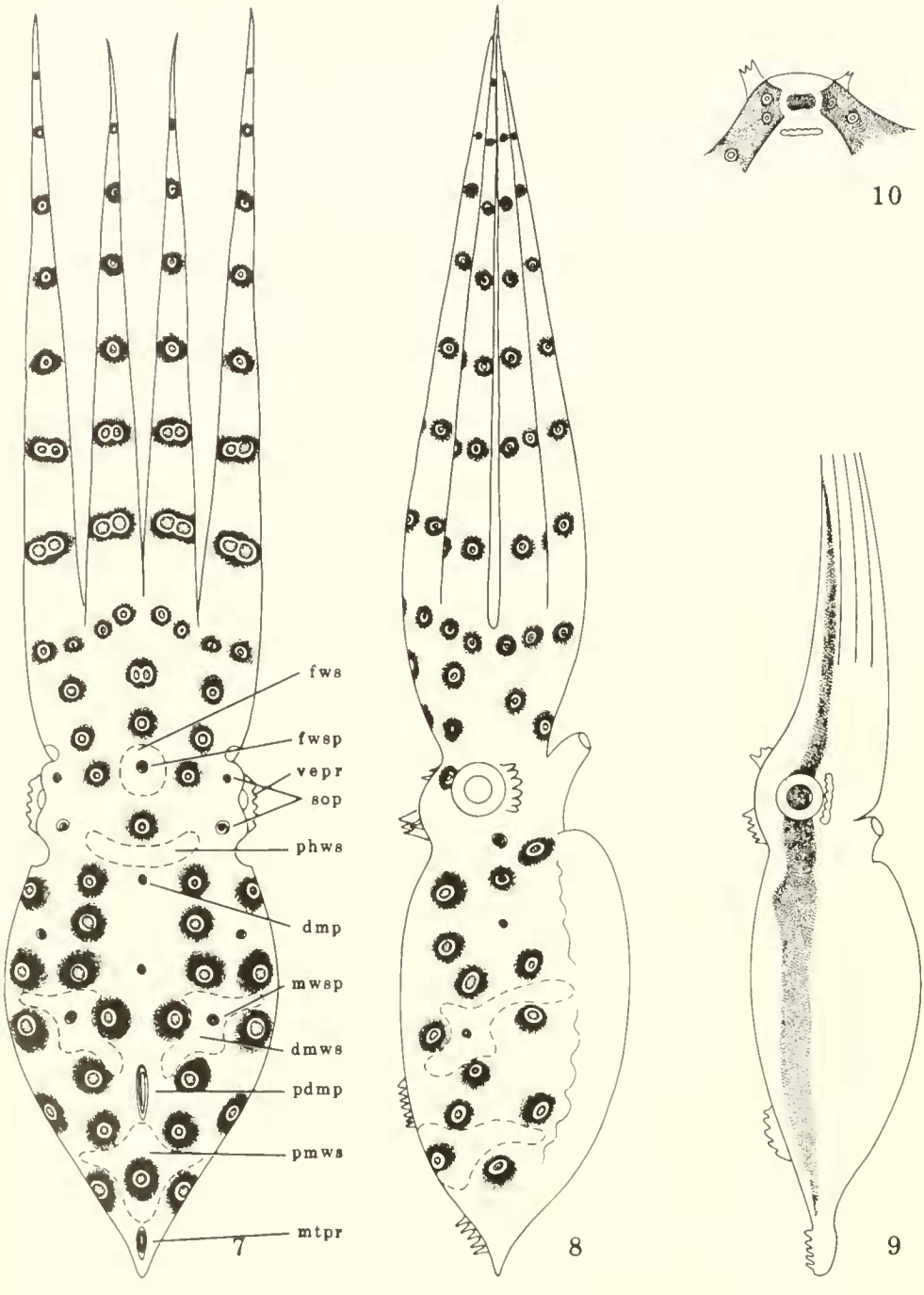
A. Synopsis

Diagnosis: Mantle small, elongate, ovoid, pointed posteriorly; mantle length to 40 mm; total length to 110 mm; total weight 40–50 g; skin papillate, with conspicuous pattern of dark elongate maculae and iridescent blue lines on mantle and dark maculae with small iridescent blue rings on head, web and arms; eyes small; arms short, 1.5 to 2.5 times mantle length, subequal; typical arm formula IV.III.II.I; suckers small, numerous, none enlarged; gills with 4 or 5 lamellae per demibranch; right arm III hectocotylized, length 95% of left arm III; end organ medium to large, 7–9–12% of hectocotylized arm length; ligula flat and smooth, calamus large; eggs 7–9 mm long.

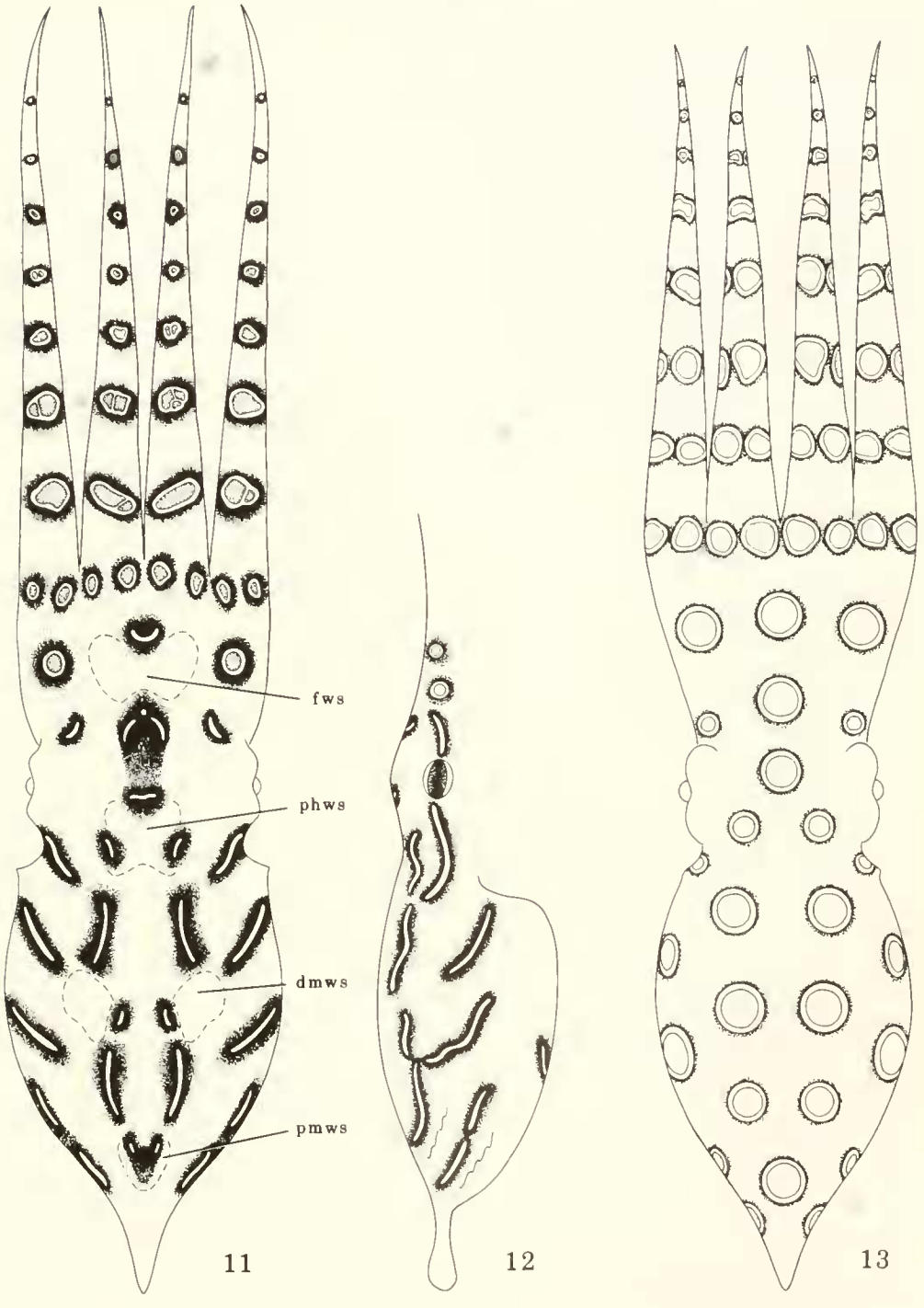
Distribution: Australian endemic. Temperate to subtropical, apparently restricted to New South Wales. Widespread in shallow, sheltered coastal waters from the intertidal zone to depths of 10 to 30 m. Typically found along rocky shores where it lives in crevices, rock pools and underwater caves. Also found in bays, living under rocks, in grass beds and in debris such as cans, bottles and empty bivalve shells (scallops, oysters and mussels).

Life history: Life span 7 to 9 months. Sexually mature at 4 months. In the Sydney area, spawning occurs in March and from September to December. 100 to 200 large eggs (7 to 9 mm) laid by female and brooded loosely in web and arms. Embryonic development takes about 60 days. Development direct; young benthic upon hatching. Food primarily crabs, but bivalves also may be eaten.

References: Anon., N.D.; McMichael, 1957, 1958, 1964, 1971; Dew, 1959; Hopkins, 1964; Lane & Sutherland, 1967; Sutherland &



FIGS. 7–10. *Hapalochlaena* cf. *maculosa*. Figs. 7, 8: Stylized dorsal (7) and right lateral (8) views to show size and distribution pattern of blue rings (clear circles) surrounded by dark maculae (black stipple), primary papillae (concentric, spiral and peaked lines) and white spots (encompassed by dashed lines). Fig. 9. Right lateral view, jetting octopus with dark lateral stripe along arms, head and mantle. Fig. 10. Right lateral view of head and eye (anterior to right) with dark lateral stripe.



FIGS. 11–13. *Hapalochlaena* cf. *fasciata*. Figs. 11, 12 and *H. lunulata*, Fig. 13: Stylized dorsal (11, 13) and right lateral (12) views to show size and distribution pattern of blue lines and rings (clear lines and circles) surrounded by dark maculae (black stipple) and white spots (encompassed by dashed lines).

FIG. 14. *Hapalochlaena* cf. *maculosa*. Attached to the green alga *Caulerpa cupressoides*, in Watson's Bay, Lizard Island. Left lateral view; note prominently erected papillae on mantle and ventral to the eye. Epiphytic gastropods are *Engina* and *Anachis*. Photograph by N. Coleman.

Lane, 1969; Deas, 1970; Freeman & Turner, 1970; Croft & Howden, 1972; Cropp, 1972; Friese, 1972; Tranter & Augustine, 1973; Reynolds, 1983; Keith, 1986; Marsh & Slack-Smith, 1986. (Note: Unless illustrations or photographs are provided, identifications in the literature cannot be relied upon with regard to *H.* cf. *maculosa* and *H.* cf. *fasciata*, hence both are combined here.)

B. Field observations

None.

C. Components of body patterns

A single individual of *H.* cf. *fasciata* (Hoyle, 1886) was observed for 14 days in an aquarium at the Australian Museum in Sydney. This species is distinct from those observed at Lizard Island (*H.* cf. *maculosa*) and the species traditionally identified as *H. lunulata*. We consider the species commonly collected in New South Wales to be *H.* cf. *fasciata*. For comparison, we present information on the color and body patterns of the New South Wales specimen (Figs. 19–25). Body proportions differ in *H.* cf. *fasciata* from those in *H.* cf. *maculosa*. The arms are longer and more attenuate and the mantle is slightly larger and more robust, although still distinctly elongate and tapered posteriorly (Figs. 19–21). The normal background coloration is a deep orange/yellow. The dorsal and lateral surfaces of the mantle are covered with a regular pattern of iridescent blue lines, not rings (Figs. 11, 12, 19–25). The lines are oriented on the body as streaks or diagonals. The ventral surface of the mantle lacks lines or rings. Small blue rings are present on the head, web and arms. Those on the arms coalesce proximally into large irregularly shaped rings or transverse figure-8's and distally into dots of blue (Fig. 11). The body can be covered with small conical and large flat papillae or papillate ridges. The morphogenetic fields or patterns of distribution of papillae appear to be similar to the Lizard Island species, *H.* cf. *maculosa*. Rows of small papillae occur in the light areas between the dark lines on the lateral mantle but not witnin the maculae. In *H.* cf. *fasciata* three to four low, connected papillae lie ventral to the eye rather than a strong, raised papillate ridge, as in *H.* cf. *maculosa*.

Behavioral responses manifest in color and body patterns are very similar to the species at Lizard Island. At rest, the cryptic pattern is a uniform light grey/beige (Fig. 22). The iridescent blue mantle lines and the head, web, and arm blue rings are visible but subdued, the maculae are absent, and the texture is finely granular with minute papillae. With increasing disturbance (Figs. 20, 23–25) the animal flushes to a uniform dark charcoal or slate grey and the iridescent blue lines and rings become very intense surrounded by maculae of very dark chromatophores. In this pattern the primary papillae may be erect and prominent.

Table 5 presents an inventory of components of body patterns currently recognized for *H.* cf. *fasciata* based upon observations and photographs of a living animal in Sydney and on the literature.

D. Discussion

A discussion of *Hapalochlaena* species appears at the end of the section on *H. lunulata*.

TABLE 4. Components of body patterns in *Hapalochlaena* cf. *maculosa*.

I. Chromatic components

A. Light
- light-colored papillae
- dorsal mantle stripe
- dorsal mid-mantle white spots (dmws, 2)
- posterodorsal mantle white spot (pmws)
- posterior head white spot (phws)
- frontal white spot (fws)
- transverse white streak (tws)

B. Dark
- dark maculae (spots on mantle, web and arms)
- dark lateral stripe

C. Other
- iridescent blue rings

II. Textural components

A. Primary papillae
- simple dorsal mantle papillae (dmp, 4)
- compound dorsal eye papillae (adep, pdep, 2/eye)
- compound ventral eye papillate ridge (vepr, 1/eye)
- compound flat posterior dorsal mantle papillate ridge (pdmpr, 1)
- compound flat posterior mantle tip papillate ridge (mtpr, 1)
- simple dorsal mantle white spot papillae (mwsp, 1/spot)
- simple frontal white spot papilla (fwsp, 1)
- extended posterior mantle tip

B. Secondary papillae
- minute simple uniform body papillae
- simple ring papillae (1 in center of each ring)
- simple intermacular lateral mantle papillae

C. Other
- granular
- smooth

III. Postural components
- radiating arms
- curled arms
- coned arms
- drooping arms
- flared web
- elongate pointed mantle
- raised head and eyes

IV. Locomotor components and maneuvers
- resting/sitting
- hovering
- scuttling
- jetting
- inking
- free fall
- burying

V. Body patterns

A. Chronic
- light cryptic mottle
- light uniform

B. Acute
- dark conflict mottle
- dark uniform (flush)
- dermatic (white blanch)
- flashing maculae and blue rings
- flamboyant

5. *Hapalochlaena lunulata* (Quoy & Gaimard, 1832)

Common name: Greater blue-ringed octopus. We introduce this name to draw attention to the large blue rings (7–8 mm in diameter) on the dorsal mantle, head, web and arms.

A. Synopsis

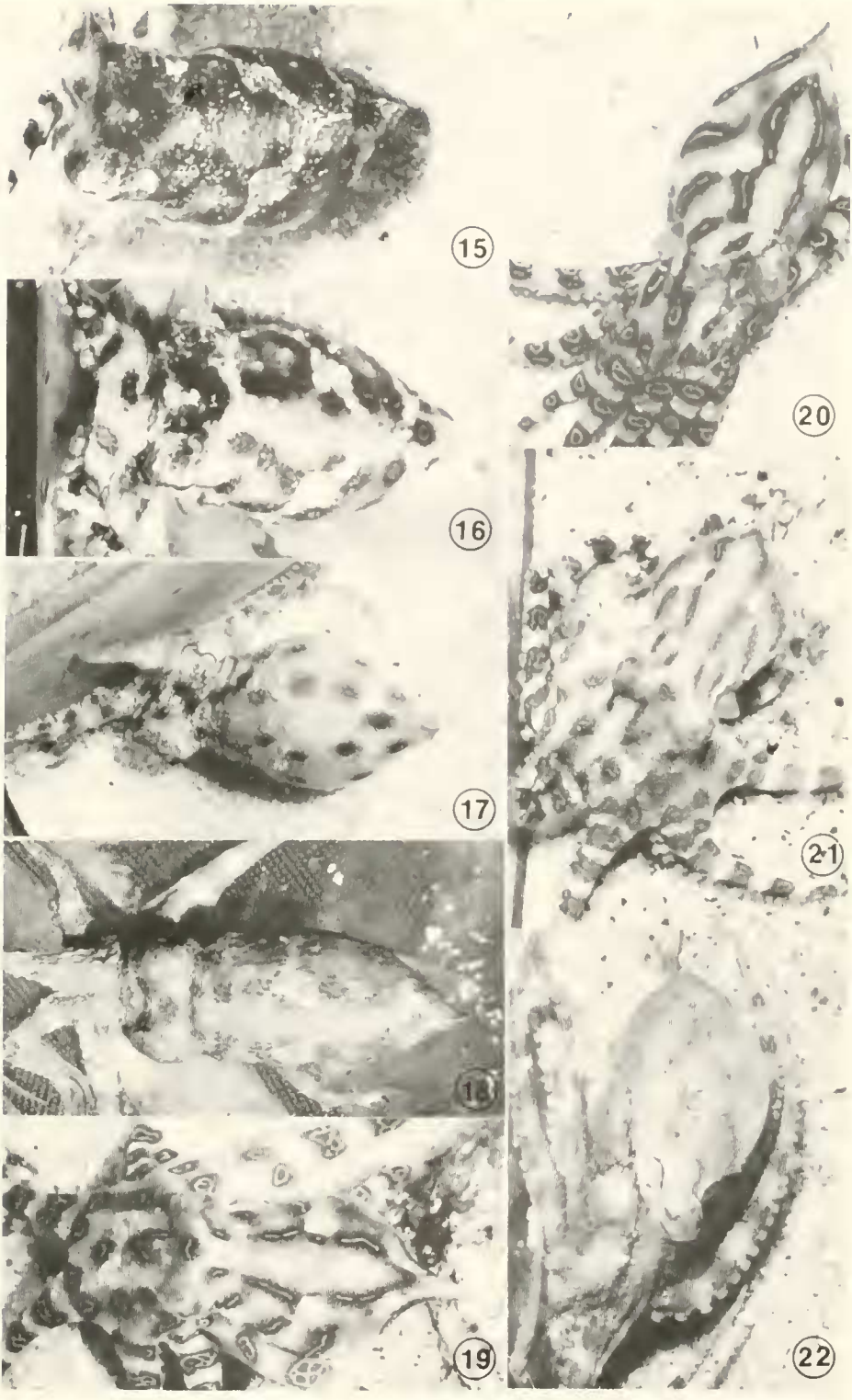
Diagnosis: Mantle ovoid, pointed posteriorly, slightly flattened dorsoventrally; mantle length to 55 mm; total length to over 100 mm; total weight to 80 g; skin soft and semigelatinous, mantle, head, web and arms with

TABLE 5. The components of body patterns in *Hapalochlaena* cf. *fasciata*.

I. Chromatic components		
A. Light	B. Dark	C. Other
dorsal mantle stripe	dark maculae (spots on web and arms)	irridescent blue lines and rings
dorsal mid-mantle white spots (dmws, 2)	dark lines (on mantle)	
posterodorsal mantle white spots (pmws)	dark orange/yellow	
posterior head white spot (phws)		
frontal white spot (fws)		
II. Textural components		
A. Primary papillae	B. Secondary papillae	C. Other
simple dorsal mantle papillae (4)	minute simple uniform body papillae	granular
compound dorsal eye papillae (2/eye)	simple intermacular lateral mantle papillae	smooth
compound ventral eye papillate ridge (1/eye)		
compound flat posterior dorsal mantle papillate ridge		
compound flat posterior mantle tip papillate ridge		
simple dorsal mantle white spot papillae (1/spot)		
simple frontal mantle white spot papilla		
extended posterior mantle tip		
III. Postural components		
radiating arms		
curled arms		
coned arms		
erect head & eyes		
elongate pointed mantle		
copulatory embrace[1]		
IV. Locomotor components and maneuvers		
resting/sitting		
scuttling		
jetting		
inking		
mating[1]		
V. Body patterns		
A. Chronic	B. Acute	
light cryptic mottle	dark conflict mottle	
light uniform	dark uniform (flush)	
	flashing maculae, blue lines and rings	
	flamboyant	

[1]Tranter & Augustine (1973).

FIGS. 15–22. *Hapalochlaena* cf. *maculosa*. Figs. 15–18, dorsal views of resting animals and *H.* cf. *fasciata*, FIGS. 19–22, dorsal views. Fig. 15. Dark mottle; blue rings completely subdued; maculae dark, expanded and coalesced; mantle and head white spots and dorsal mantle white stripe expressed but subdued. Fig. 16. Light mottle; blue rings and maculae expressed, especially on right side (top) facing disturbance; all mantle and head white spots expressed. Fig. 17. Light uniform; blue rings expressed; maculae subdued, separate. Fig. 18. Dark uniform; blue rings greatly subdued; maculae expanded and coalesced. Fig. 19. Scuttling locomotion while disturbed; blue lines and rings and maculae dark, expressed moderately; mantle, head and frontal white spots evident. Fig. 20. Warning pattern; blue lines and rings expressed vividly; maculae dark, white spots subdued to absent. Fig. 21. Resting after disturbance; blue lines and rings expressed moderately; maculae subdued; white spots subdued. Fig. 22. Resting position; light uniform; blue lines and rings very subdued; maculae absent; no white spots expressed except subdued frontal spot; mantle tip rounded.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conspicuous pattern of large iridescent blue rings (7–8 mm in diameter) with broad dark maculae around the outer periphery and clear centers; eyes small; arms short, 1.5 to 2 times mantle length, subequal; typical arm formula IV.III.II.I; suckers few, level with oral surface of arms; gills with 7 to 9 lamellae per demibranch; right arm III hectocotylized, length 80 to 90% of left arm III; end organ medium-sized, 7 to 9% of hectocotylized arm length; ligula flat, smooth, with slightly elevated edges; calamus small, open; eggs 2.5 to 3.5 mm long; hatchlings planktonic.

Distribution: Widely distributed throughout the Indo-West-Pacific and Indian Oceans. Australia, New Guinea, Philippines, Sri Lanka, Vanuatu Is., Solomon Is., Misal Is., Andaman Is. In Australia the species has been recorded in Queensland, Northern Territory, and Western Australia. Little information is available on vertical distribution and habitat.

Life history: Life span not known. In the Philippines, spawning occurs in March and April. 60 to 100 small eggs laid by female and attached to substrate in festoons of about 20 eggs each. Embryonic development takes about 25 to 35 days. Hatchlings are briefly planktonic prior to becoming benthic. Species feeds actively on crabs and bivalves.

References: Adam, 1954; Flecker & Cotton, 1955; McMichael, 1957, 1971; Overath, 1973; Overath & Boletzky, 1974; Marsh & Slack-Smith, 1986; Wells & Bryce, 1986.

B. Field observations

None.

C. Components of body patterns

Not observed in life. This very distinct species has been studied by us only from color transparencies of live animals provided by C. Bryce and A. Kertstich (Figs. 29, 30). The drawing (Fig. 13) was developed from a photograph by Kertstich to contrast the general body pattern of *H. lunulata* with the patterns of the two species we observed alive. Photographs of live animals appear in Wells & Bryce (1986) and in Marsh & Slack-Smith (1986).

Discussion of *Hapalochlaena* spp.

The genus *Hapalochlaena* is a complex of octopuses with small bodies, short arms and shallow webs. The genus is further characterized by the unique presence of iridescent blue rings or lines set in macula of dark chromatophores. Observations were made on live animals of two very distinct species of *Hapalochlaena*, one from Lizard Island, the other from near Sydney. When observed alive or from color photographs, these two species are very easy to distinguish, whereas preserved specimens may be less distinctive. In fact, the study of living animals and of color photographs of living animals has enabled us to recognize species differences and thus to

FIGS. 23–31. *Hapalochlaena* cf. *fasciata*, Figs. 23–25, dorsal views; *H.* cf. *maculosa*, Figs. 26–28, dorsal and left lateral views; *H. lunulata*, Figs. 29–30, dorsal and left lateral views, and *Octopus cyanea*/*O. ornatus*, Fig. 31, lateral views. Fig. 23. [top row, left] Light mottled (grey phase); blue lines and rings expressed; maculae expressed lightly; mantle, head and frontal white spots expressed. Fig. 24. [top row, center] Dark mottle; blue lines and rings expressed vividly; maculae dark, expanded and coalesced; frontal white spot visible, other white spots suppressed. Fig. 25. [top row, right] Light mottle (beige/yellow phase); blue lines and bars expressed; maculae dark and separate; white spots suppressed. Fig. 26. [middle row, left] Moderate warning pattern of Lizard Island animal; blue rings expressed; maculae expanded dark and coalesced on right side facing disturbance (left of image), otherwise subdued; mantle white spots visible. Fig. 27. [middle row, center] Deimatic pattern; blue rings and black maculae expressed vividly; texture finely papillate. Photograph by C. Bryce (Shark Bay, Western Australia). Fig. 28. [middle row, right] Scuttling locomotion; warning pattern; blue rings expressed vividly; black maculae expanded very dark and coalesced. Photograph by C. Bryce (Albany, Western Australia). Fig. 29. [third row, left] Deimatic pattern; blue rings vivid; maculae expressed minimally as black rings outside of blue rings, centers light. Photograph by C. Bryce (Exmouth Gulf, Western Australia). Fig. 30. [bottom row, left] Deimatic pattern; blue rings vivid; dark macular rings expanded around outside of blue rings, centers dark. Photograph by A. Kerstitch (Vanuatu Islands). Fig. 31. [bottom row, right] *Octopus cyanea* (right) in light uniform pattern (deimatic) with vivid ocellus and smooth texture. *Octopus ornatus* (left) with white streaks on mantle and white spots on arms against maroon background. Photograph by W. F. van Heukelem (Honolulu, Hawaii).

begin resolving problems that have puzzled investigators since the original descriptions of the nominal species over 100 years ago.

While a great deal of work remains to be done, we have been able to distinguish at least three species based upon the size and configuration of their iridescent blue markings. Many living and preserved specimens from localities over the entire geographic range of the genus must be examined to make final judgments and decisions. At present, we concur with the identifications provided by S. S. Berry (in Halstead, 1965) and recognize the following distinct species:

1. *Hapalochlaena* cf. *maculosa* (Figs. 7–10) is characterized principally by small blue rings, 1–2 mm in diameter, on the dorsal and lateral (but not ventral) surfaces of the mantle, head, web and arms. This species occurs at Lizard Island and similar small-ringed forms have been recorded from numerous localities in Australian and Indonesian waters. Small-ringed forms may represent a widely distributed species, but more likely a species complex is involved, since in at least one area the ventral mantle of specimens examined is partially covered with a number of blue rings. This is the *maculosa* type of blue-ringed octopus originally described by Hoyle in 1883.

2. *Hapalochlaena* cf. *fasciata* (Figs. 11, 12) is characterized by short, blue lines (streaks and diagonals) on the mantle and by very small blue rings (single circles, figure-8's or complex circular designs) on the head, web and arms. The configuration and distribution of blue lines and rings is comparable in general terms to that of the lesser blue-ringed octopus. This is the species we studied from waters near Sydney. It has been referred to repeatedly as *H. maculosa* in the literature. However, all the specimens we have examined from New South Wales have blue lines not rings and, hence, the specific name *fasciata* Hoyle, 1886 seems applicable. The extent of its distribution is unknown because it has been frequently confused with the "*maculosa*" species.

3. *Hapalochlaena lunulata* (Fig. 13) is distinguished by relatively large blue rings up to 7 or 8 mm in diameter on the dorsal and lateral surfaces of the mantle, head, web and arms. This species also seems to be widely distributed in Australian and central Indo-Pacific waters. A complex of species or subspecies may be involved that can be resolved only by further critical study.

What could be the function of the brilliant, iridescent blue displays of *Hapalochlaena*? Judging from the behavioral responses to disturbance or threat, these seem to be a form of warning coloration with which these small octopuses signal their unpleasant taste or poisonous bite. Interestingly, there are several other vividly marked small octopuses (e.g. *Octopus zonatus, O. chierchiae*), but it is not known whether they also are poisonous.

Surprisingly, reference to color and body patterns in the *Hapalochlaena* complex is very limited. The majority of reports detail the blue rings and dark spots or maculae on the body and arms. Although several photographs show animals with distinct lines on the mantle, the animals still are referred to as the "blue-ringed octopus." On the basis of photographs in published reports we can identify the following: *H.* cf. *maculosa*—Reynolds, 1983; Marsh & Slack-Smith, 1986; *H.* cf. *fasciata*—Sutherland & Lane, 1969; Deas, 1970; Hal-

FIGS. 32–42. *Sepia papuensis*, Figs. 32–35, right lateral and dorsal views; *Metasepia pfefferi*, Figs. 36–41, right lateral and dorsal views, and *Metasepia tullbergi*, Fig. 42, right lateral view. Fig. 32. [top row, left] Bipod position; dark mottle on dorsal mantle, light mottle on ventral mantle; dorsal mantle dark spot prominent; lateral mantle white spots expressed against light background. Fig. 33. [second row, left] Bipod position, dark mottle on dorsal and ventral mantle; head, mantle and finline white spots conspicuous. Fig. 34. [top row, center] Light mottle approaching light uniform; unilateral dorsal mantle dark spot directed toward source of disturbance; dorsal mantle white spots expressed. Fig. 35. [top row, right] Dark mottle. Fig. 36. [third row, left] Tripod posture; raised arms I; diagonal mantle white bars, finline white stripe, lateral mantle white spots expressed; head and arm light components expressed; yellow and magenta absent. Fig. 37. [fourth row, left] Ambling locomotion on ambulatory flaps and arms IV; right arm IV down, left arm IV raised to take next step; flamboyant body pattern; yellow and magenta expressed. Fig. 38. [middle row, center] Dark uniform with diagonal mantle white bars expressed; yellow and magenta absent. Fig. 39. [middle row, right] Passing wave pattern, especially on left side of mantle; first anterior wave in mid-cycle, second anterior wave originating at anterior mantle margin; posterior wave originating at posterolateral margins of mantle. Fig. 40. [bottom row, center] Prone position with flanged fins and flattened arms; yellow and magenta expressed. Fig. 41. [bottom row, right] Head-on view of flamboyant arm pattern; suckers enveloped by yellow protective membranes. Fig. 42. [bottom row, left] Flamboyant pattern of color, texture and posture; note ambulatory flap. Photograph of Japanese animal by T. Koyama, courtesy of T. Okutani.

TABLE 6. The components of body patterns in *Metasepia pfefferi.*

I. Chromatic components

A. Light
- arm IV white spots (aws IV)
- arm III white spots (aws III)
- arm I white spots (aws I)
- web white spots (wws)
- dorsal head white spots (dhws)
- dorsal head white triangles (dhwt)
- lateral head light field (lhlf)
- dorsal mantle white bars (dmwb)
- dorsal mantle light field (dmlf)
- finline white stripe (flws)
- lateral mantle white spots (lmws, ventral to fin)
- ventral mantle white spots

B. Dark
- dorsal head dark field (dhdf)
- lateral mantle dark fields
- posterior mantle dark spot (pmds)
- dorsal mantle dark spots (dmds) (eye spots of deimatic pattern)
- arm IV dark stripe (ads)

II. Textural components

A. Primary papillae and flaps
- anteroventral eye papilla (avep, 1/eye)
- anterodorsal eye papilla (adep, 1/eye)
- posterodorsal eye papilla (pdep, 1/eye)
- finline papillae (flp 1, 5–7/side)
- laterodorsal mantle papillae (ldmp, 2 pairs)
- anterodorsal mantle papilla (admp, 3)
- posterodorsal mantle papillae (pdmp, 1 pair)
- posterodorsal mantle flaps (pdmf, 1 pair)
- mid-dorsal mantle flaps (mdmf, 1 pair)
- mantle white bar flaps (mwbf, 1 pair)

B. Secondary papillae
- dorsal head papillae
- dorsal mantle papillae
- finline papillae (flp2, 5/side)
- lateral mantle white spot papillae

III. Postural components
- arms I raised
- arms IV lowered (tips on substrate)
- flamboyant arm splay
- drooping arms (while hovering)
- raised head
- flanged fin (folded down)
- flattened/flared arms
- bent arms IV (while ambling)
- bipod (body off bottom)
- tripod (posterior mantle on bottom)
- prone (body flat on bottom)

IV. Locomotor components and maneuvers
- resting
- floating
- hovering
- swimming
- jetting
- ambling
- inking

V. Body patterns

A. Chronic
- light cryptic mottle
- light uniform

B. Acute
- dark conflict mottle
- dark uniform (flush)
- flamboyant
- passing wave (apw, ppw, 1,2)
- deimatic

stead & Danielson, 1970; Voss, 1971; Cropp, 1972; Tranter & Augustine, 1973; Keith, 1986; *H. lunulata*—Robson, 1929 (pl. 4, fig. 1); Flecker & Cotton, 1955; Anon., 1968; Marsh & Slack-Smith, 1986; Wells & Bryce, 1986.

Brief descriptions of color in adults and hatchlings of *H.* cf. *fasciata* were provided by Dew (1959) and Tranter & Augustine (1973), who found that the characteristic blue lines and rings of *H.* cf. *fasciata* appeared 6 weeks after hatching, although the macula pattern developed at an age of 3 or 4 weeks. The postures and activities associated with mating were described by Tranter & Augustine (1973) but patterns of color specific to courtship and mating were not mentioned.

Species of the subfamily Octopodinae are all very similar morphologically and anatomically. Hence, few supraspecific taxa have been erected to help subdivide an enormous number of seemingly uniform species. The fixed and characteristic markings observed in *Hapalochlaena* lead us to conclude that this species complex should be recognized as distinct at the generic level.

Morphogenetic patterns, especially of color and texture, are fixed, conservative characters within families and genera. Although more research is needed, this phenomenon will add a whole new suite of genetically stable characters upon which to base systematic analyses, diagnoses of species and genera, etc. The elucidation of these morphogenetic patterns, through study of living animals or color photographs of living animals, will provide valuable information for understanding both the systematics and behavior of cephalopods, and for identification of species in the field.

6. *Metasepia pfefferi* Hoyle, 1885

Common name: Pfeffer's flamboyant cuttlefish. We name this species after the German teuthologist Georg Pfeffer. "Flamboyant" emphasizes the striking, flowery body patterns of the genus *Metasepia*.

A. Synopsis

Diagnosis: Mantle very broad, oval; mantle length to about 80 mm; total length to about 160 mm; dorsal mantle with 3 pairs large, primary flat, flap-like papillae and 1 pair prominent mantle white bars; head with primary papillae over eyes; arms broad, blade-like; fins broad, transparent; tentacular club short, with swimming keel twice as long as club; dorsal and ventral protective membranes separate on tentacular stalk; club suckers very few in number, in about 5 transverse rows, with 3 or 4 median suckers enormously enlarged; cuttlebone broad, rhomboidal, shorter than mantle; dorsal surface completely chitinized, without median rib or spine.

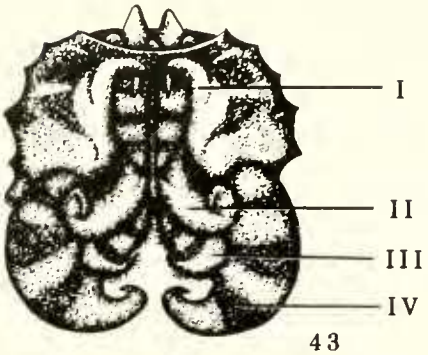
Distribution: Tropical Australian waters: Arafura Sea (type locality), Queensland (Capricorn group, Moreton Bay—Alan Jones, personal communication) to Western Australia (to about 33°S). Shallow-water species on sand/silt bottom to about 50 m.

Life history: Unknown. This paper is the first report of observations on living animals.

References: Hoyle, 1885b, 1886; Adam & Rees, 1966; Adam, 1979; Lu & Phillips, 1985; Wells & Bryce, 1986.

B. Field observations

Two juvenile *M. pfefferi* were captured in 10 to 13 m at separate locations during daytime dives in Watson's Bay (CFER-22 and CFER-42). In both localities, the flat bottom was composed of a mixture of sand and silt, devoid of rocks and rubble. The bottom was inhabited by a large number of black holothurians, *Holothuria* sp., a few brown-yellow holothurians, and dense patches of attached green algae: a calcareous species of *Halimeda* and scattered *Caulerpa cupressoides*. In its natural habitat, *M. pfefferi* looks like anything but a cuttlefish. When first observed and prior to capture, animal 1 was variously identified by divers as a small frilly crab, a crayfish, a pufferfish or a piece of alga slowly moving or drifting along the bottom. Even when the divers knew what to look for during subsequent dives, recognition of animal 2 was difficult. When first observed it was hovering in a stationary position 10 cm above the bottom, motionless except for gentle mantle undulations. Upon sighting the diver, it swam to the bottom and assumed a cryptic pattern that matched the beige/grey color of the sandy silt substrate. When pursued and captured, the animal changed to a vivid black and yellow color pattern and a distinctly papillate texture. *Metasepia pfefferi*'s ability to conceal itself is due both to the vivid and exaggerated color and textural patterns as well as the unusual configuration of the arms (described below). Observations of behavior and body patterns in aquaria were consistent with those observed in the field.



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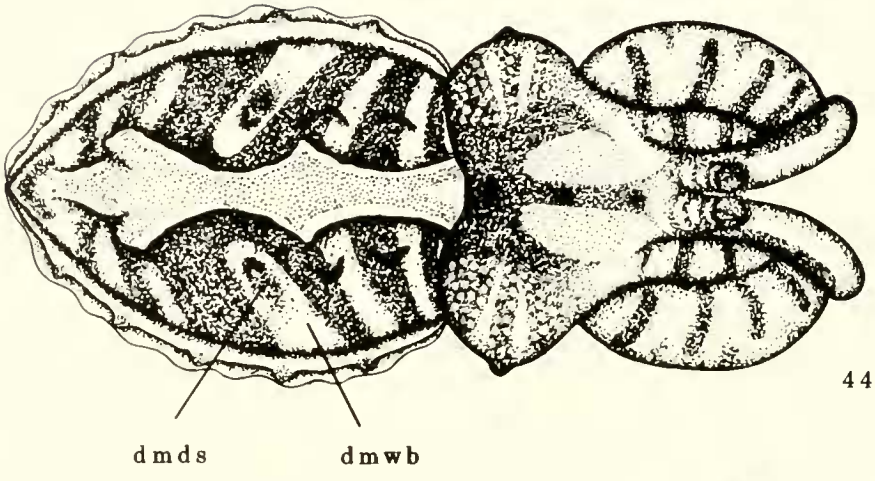

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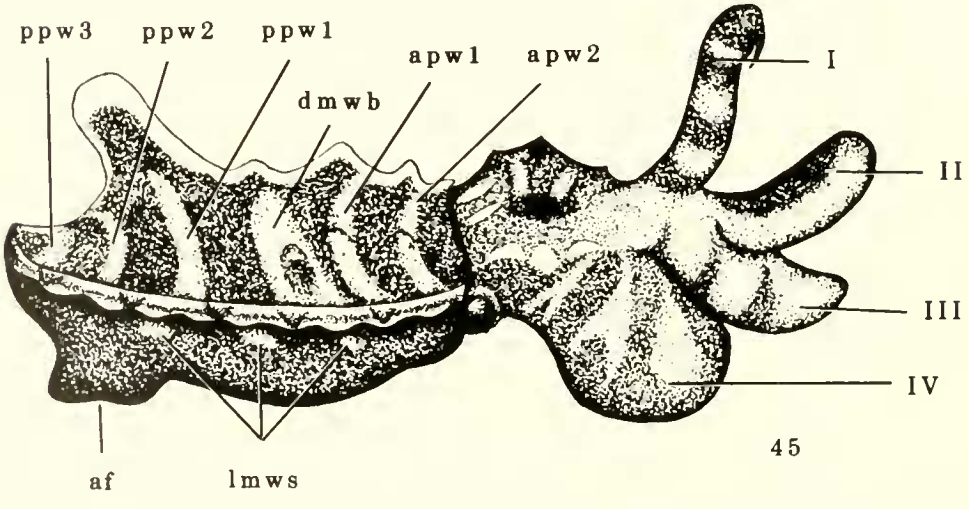

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FIGS. 43–45. *Metasepia pfefferi*. Field drawings to show texture, flamboyant configuration of arms and color patterns on mantle during passing wave pattern. Fig. 43. Head-on view; arm configuration observed while in bipod, tripod and prone postures. Fig. 44. Dorsal view. Fig. 45. Right lateral view; prone posture; note ambulatory flaps (shown shorter than normal). Drawings by B. Morton of Lizard Island animal in aquarium.

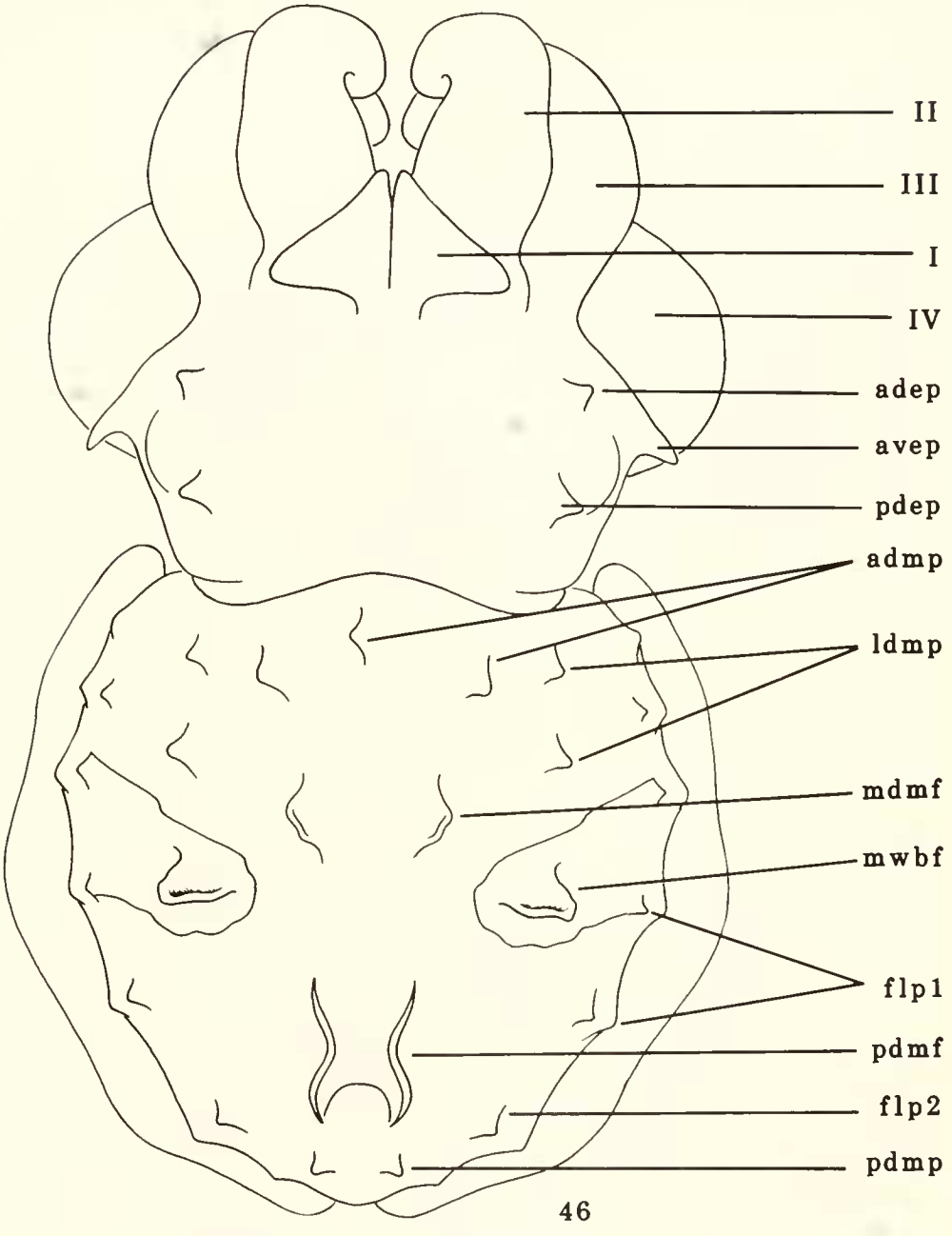
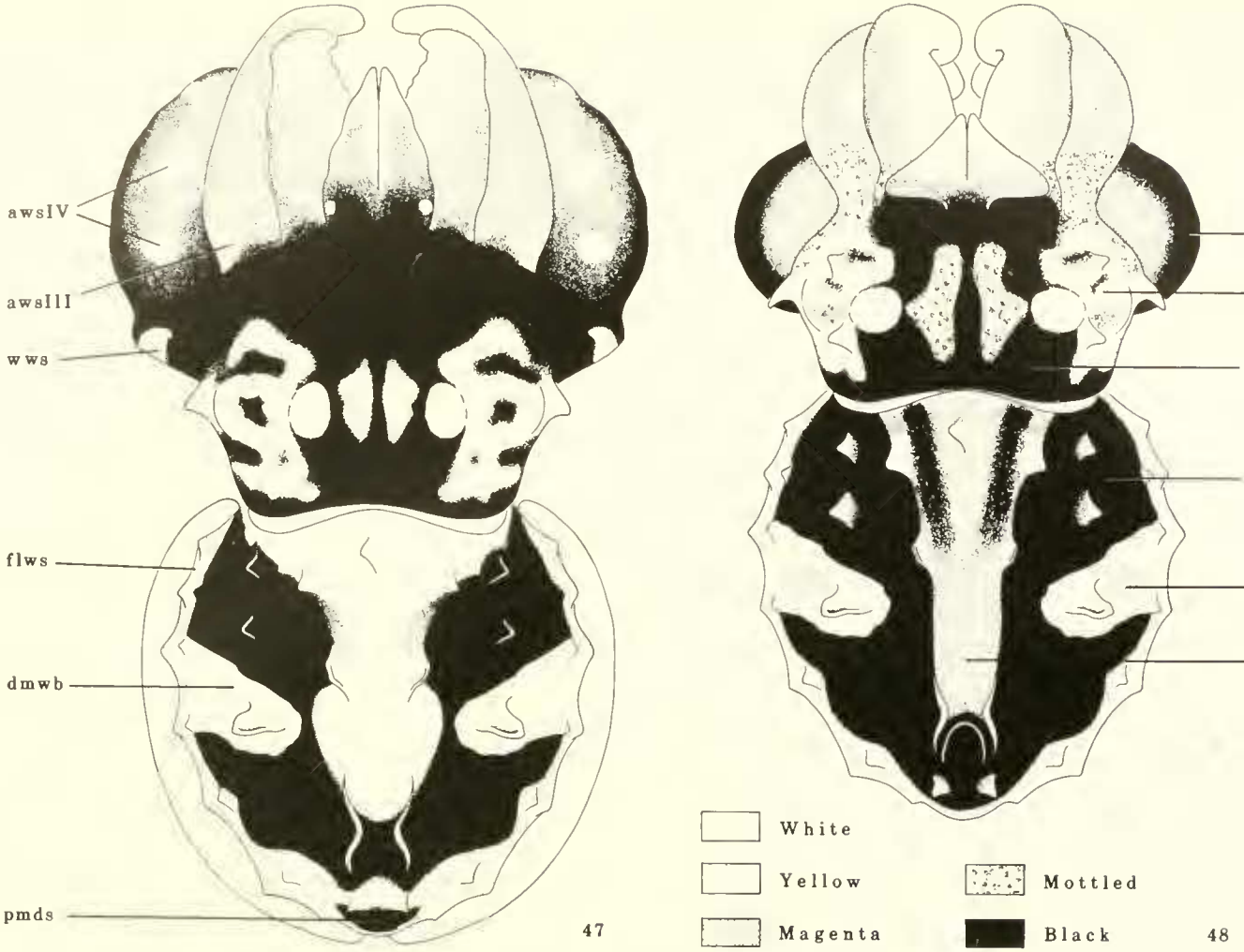


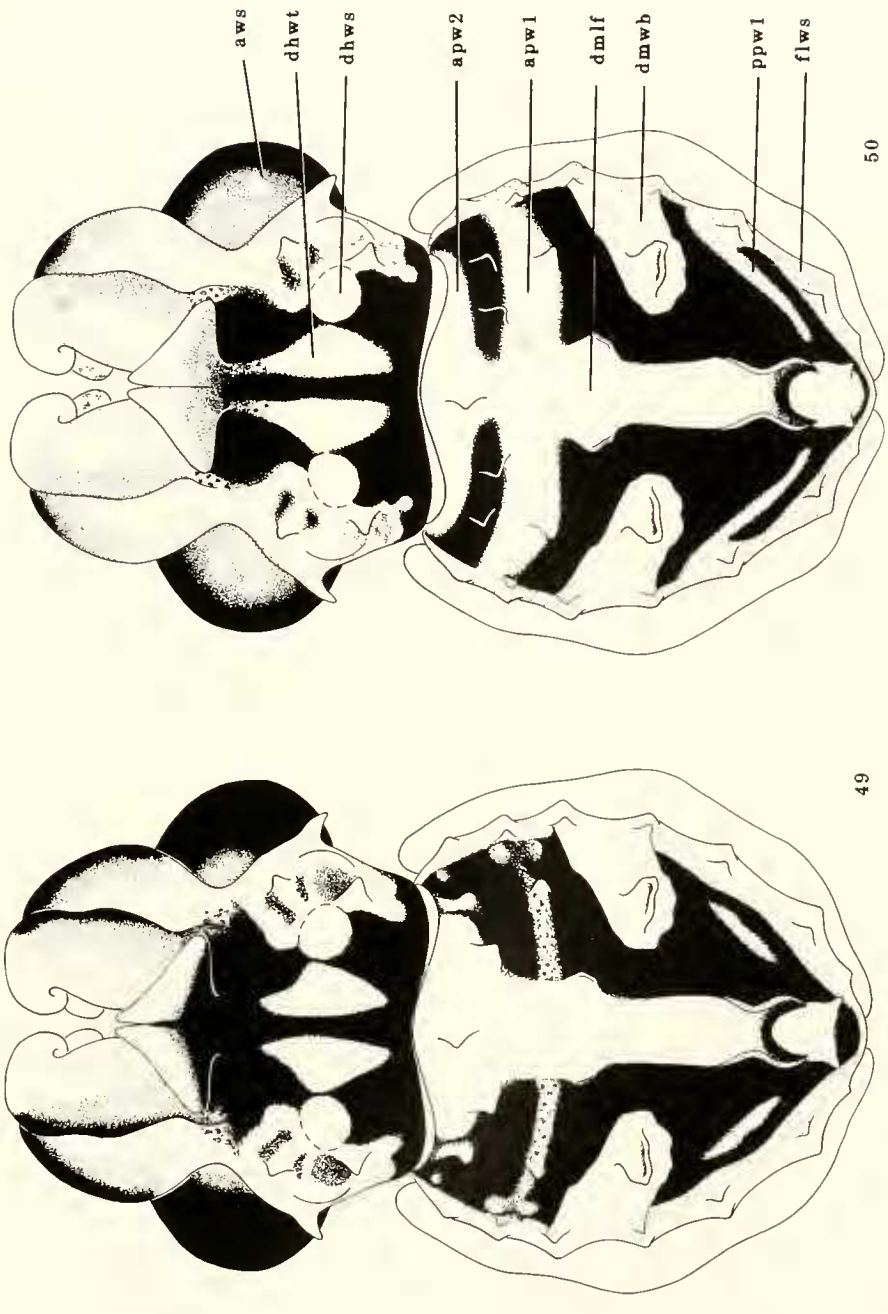
FIG. 46. *Metasepia pfefferi:* Stylized dorsal view showing location of large, primary papillae and flaps and smaller secondary papillae.

C. Locomotion

In addition to floating, hovering, swimming and jetting, *M. pfefferi* moves along the bottom by means of a remarkable new type of locomotion we term "ambling." This mode of locomotion is aided by a pair of muscular flaps along the margin of the posterior third of



FIGS. 47–48. *Metasepia pfefferi.* Stylized dorsal views to show color and body patterns in arms flared (47) and flanged fin (48) patterns.



FIGS. 49–50. *Metasepia pfefferi*. Stylized dorsal views to show color and body patterns during two phases of the passing wave pattern.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the ventro-lateral mantle (Figs. 37, 45, 58, 59). The flaps, which look like a pair of elongate, ventrally-directed fins, border the edge of the ventral "suction" disk. They are grey to beige in overall color with two indistinct pale yellow vertical bands. We term these structures "ambulatory flaps," to denote their function in this unusual mode of locomotion.

The ambulatory flaps are erect most of the time, whether the animals are resting, swimming, hovering or ambling. At rest the animals sit tripod-fashion (Fig. 36) on the erected ambulatory flaps and on the ventrally directed ventral arms. The tips of the ventral arms typically are flattened and curled medially giving the appearance that the animals are resting on their "forearms" (Fig. 41). In this position the head and mantle opening are elevated well above the bottom.

The animals amble in a "slow walking" motion along the bottom using the ventral arms as "legs." The ambulatory flaps participate by sliding or shuffling forward alternately in sequence with the ventral arms (Figs. 37, 58, 59). This locomotion pattern is similar to the gait of a quadruped vertebrate in that the right ventral arm in front and the left ambulatory flap in the rear move forward, followed by the left front arm, right rear flap. The movement is slow and deliberate, resembling an amble or a shuffle. By reversing the sequence the animals are able to move backwards. When approached from the head end, the animals amble backward rather than jetting away as is typical of most other cuttlefishes.

Finally, *M. pfefferi* can amble sideways when threatened from the side. Side stepping also is quite slow and deliberate. In moving to the right, for example, the body is supported on the right ventral arm and the right ambulatory flap. The left ventral arm and flap are swung toward the midline and set down in place. The weight then is shifted to the left arm and flap and the "appendages" on the right side are swung out to the right and placed on the substrate.

Many details of the fascinating new "ambling" behavior of *M. pfefferi* still remain to be worked out, but these original observations leave no doubt that this type of locomotion is normal for this species. In fact, it seems to be preferred, as the animals were seldom observed to swim.

D. Components of body patterns

Figs. 43 to 50 and Table 6 indicate the location and terminology of the various color, textural and postural components discussed below.

When resting or sitting on the bottom, the animals assume one of three basic postures. (1) As an animal moves into the resting position it hovers just above the bottom (Fig. 60), lowers the ventral arms to a vertical position, then settles into a "bipod" position with the weight supported on the tips of the two lowered ventral arms; it may remain in the bipod position for some time. (2) In the "tripod" position, the body is supported by the ventral arms and the posterior mantle, which rests on the ambulatory flaps in contact with the bottom (Figs. 36, 37, 57). The head and anterior mantle are elevated, arms II and III are splayed apart and arms I are raised dorsally and held together with the tips curled ventrally (Figs. 36, 37, 57). Arms IV may be either straight or curled at the tips. When the arms are all splayed out, and variously flattened and curled, the resemblance to a plant is striking (Fig. 41). (3) In the "prone" resting position, the entire ventral surface of the mantle is in contact with the bottom, and the ventral arms are horizontal with the bottom. In this position the head and anterior mantle are not elevated.

In these resting positions, the skin is sculptured with a complex pattern of primary and secondary papillae characteristic of the genus. Primary papillae and flaps are large and tonically erect (Figs. 36, 37). They may be colored solid white or yellow or tipped in white or yellow. The primary papillae include the dorsal and anteroventral eye papillae, the five to seven lateral mantle papillae on each side

FIGS. 51–60. *Metasepia pfefferi*, dorsal and right lateral views. Figs. 51–54. Passing waves, various stages; note papillate and chromatic pattern on head and arms. Fig. 55. Dark chromatic phase with subdued dorsal head white triangles and dorsal mantle white stripe; flanged fins. Fig. 56. Flamboyant color, texture and posture; dorsal mantle dark spots prominent. Fig. 57. Tripod position, flamboyant arm splay. Fig. 58. Ambling locomotion, both arms IV on bottom. Fig. 59. Ambling locomotion, left arm IV set, right arm IV raised to take step. Note ambulatory flaps in figs. 57–59. Fig. 60. Moving off bottom with drooping arms IV; ambulatory flaps reduced, edges covered with sand.

just dorsal to the insertion of the fin, two pairs of flat dorsal mantle flaps, a field of seven conical papillae on the anterior dorsal mantle and a pair of cup-shaped flaps located in the center of the mantle white bars. A discrete series of smaller conical secondary papillae is located in parallel with the primary papillae especially along the finline (Fig. 39).

The overall color of undisturbed animals is a uniform pale grey-white that matches the sandy silt background. The protective membranes on the arms are closed over the sucker rows and are striped in pale yellow (Fig. 41). When animals are disturbed slightly the head and dorsal mantle change to a highly contrasting black and white body pattern with pale yellow along the finline (e.g. Figs. 39, 47, 51–54). The dorsal head white triangles and the broad dorsal midline white stripe may be masked with black chromatophores (Figs. 38, 55). Yellow or magenta are not expressed except along the protective membranes. "Passing waves" may move over the dorsal mantle (see details below). The fins lack chromatophores and always appear transparent. When animals are disturbed repeatedly the lateral stripe above the fins, the finline stripe, turns bright yellow and the yellow of the protective membranes and the oral surfaces of the arms is intensified (Figs. 39, 40, 56).

The dorsal mantle is black and partitioned distinctly by the white midline stripe and the intense mantle white bars; mantle dark spots may be expressed (Fig. 56). The lateral mantle, ventral to the fins, is black with yellow/orange spots outlined in darker orange (Fig. 36). The ventral mantle is a uniform pale grey with a single white spot posteriorly. The dorsal head white spots are intense white; the dorsal head white triangles may be yellow or white and the dorsal eye patches are white mottled with black (Figs. 39, 40). The arms often are flattened. The aboral edges of arms I–III are magenta, the mid-regions are white and the oral edges bright yellow. The tips are pale yellow. Arms IV are dark brown/purple fringed and mottled with white. A distinct patch of yellow occurs on the aboral edge of arms III. This appears to be related to the flamboyant pattern described in juveniles of other genera of cuttlefishes and octopuses.

Often while the disturbed animals are in this color and body configuration, a series of "passing waves" washes over the surface of the dorsal mantle (Figs. 39, 49–54). This is seen as a band-like wave of white that moves through the dark field of the mantle dorsal to the fins. The white midline stripe is not affected. As one transverse wave originates at the anterior mantle margin and moves posteriorly, another wave originates on the sides of the posterior mantle and moves anteriorly until the two waves meet and disappear in the region of the mantle white bars. A second set of waves typically is generated before the first set is extinguished (Figs. 39, 50), so it is possible to see for an instant four passing waves, two moving posteriorly and two moving anteriorly.

When the fins are used to hover in a stationary position the body is oriented horizontally to the bottom and the arms either are splayed out as described above or held together in a ventrally drooping position (Fig. 60). At times the arms are extremely flattened dorso-ventrally and flared out laterally (Figs. 40, 47). In this posture the color pattern may be either a high contrast black and white or a pattern of black, white, yellow and magenta.

Metasepia pfefferi typically rests on or hovers just above the bottom. When disturbed the animals generally "amble" away and were only rarely observed to swim or jet through the water when prodded repeatedly with a rod or finger. When they do swim or jet the primary papillae and dorsal mantle flaps are erect over the entire body and the color is either a pale uniform beige/white or a vivid black, white, yellow and magenta as described above.

Some variations on these basic patterns are seen in the photographs. It is important to stress that our observations were brief and hence represent only a preliminary inventory of the chromatic, textural and postural components shown by this species. To develop a more complete body pattern inventory that can be used for comparison with other genera and species of cuttlefishes, additional effort in the laboratory and field is needed.

E. Discussion

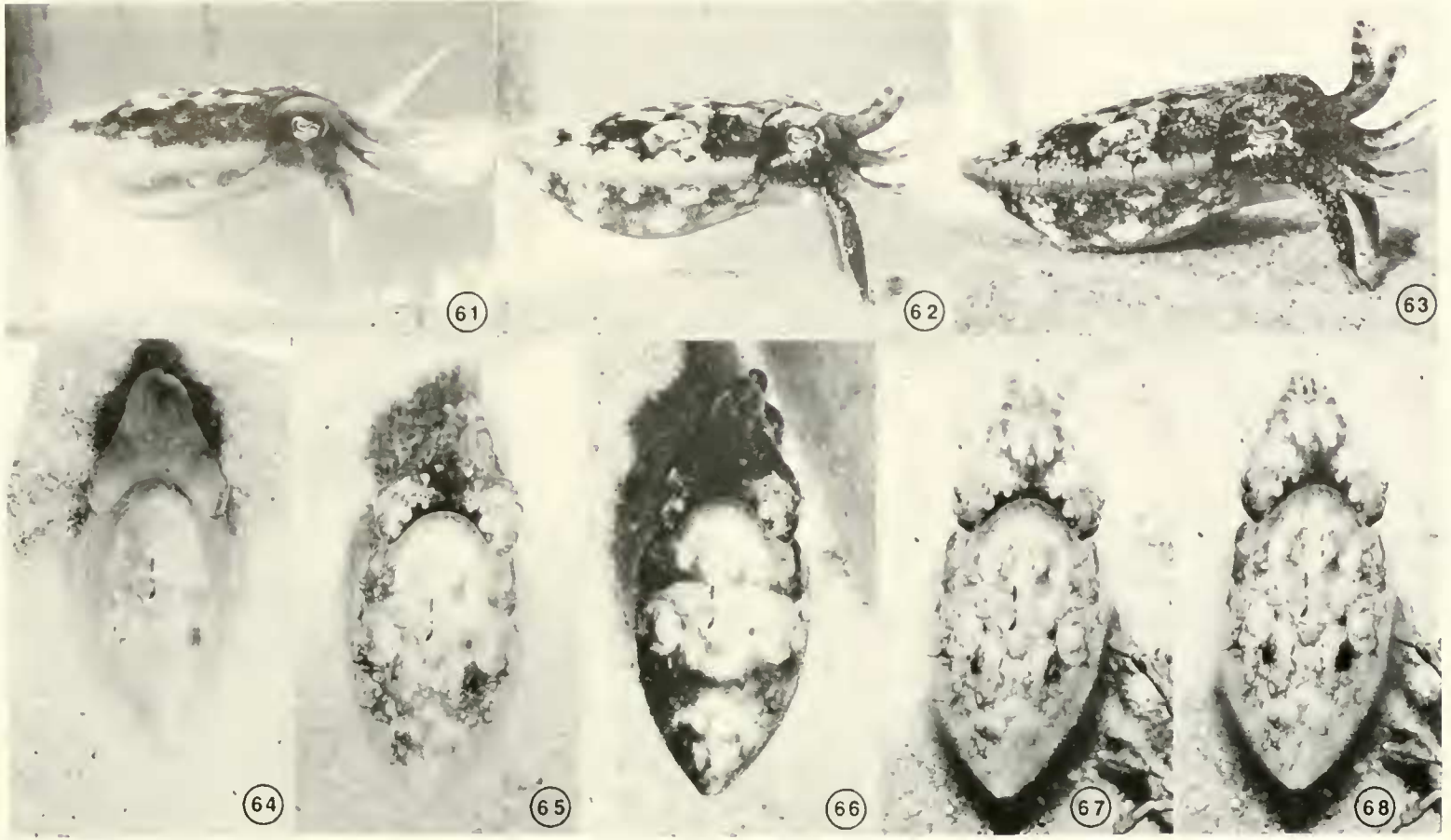
The studies on *M. pfefferi* at Lizard Island represent the first and only detailed observations of live animals published since its original description in 1885. A photograph of a live animal is published in Wells & Bryce (1986). Working from the framework provided by Hanlon & Messenger (1988) for young *Sepia officinalis*, we have been able to recognize over 50 chromatic, textural, postural and locomotor components based upon observa-

TABLE 7. The components of body patterns in *Sepia papuensis*.

I. Chromatic components		
A. Light	B. Dark	
dorsal mantle white spots	dorsal mantle dark spots (eye spots of deimatic pattern)	
dorsal mantle white stripe	dark uniform	
finline white spots	dark mottle	
finline white stripe	lateral mantle dark fields	
lateral mantle white spots (ventral to fin)	dorsal head dark field	
dorsal head white patch		
dorsal head white bar		
lateral head white stripe		
II. Textural components		
A. Primary papillae	B. Secondary papillae	C. Other
mantle white spot papillae (1/spot)	dorsal head papillae	smooth
dorsal eye papillae (2/eye)	dorsal mantle papillae	
anterodorsal mantle papillae	finline papillae (inner row)	
finline papillae (outer row)	lateral mantle white spot papillae	
dorsal mantle flaps (1 pair)	arm papillae	
	dorsal eye lid papillae (1/eye)	
III. Postural components		
bipod (body off bottom)		
tripod (posterior ventral mantle on bottom)		
prone (body flat on bottom)		
arms I raised		
arms IV lowered		
splayed arms		
flanged fin (folded down)		
IV. Locomotor components and maneuvers		
resting		
floating		
hovering		
swimming		
jetting		
burying		
inking		
V. Body patterns		
A. Chronic	B. Acute	
light cryptic mottle	dark conflict mottle	
dark cryptic mottle	dark dorsal mantle (flush)	
light uniform	dark uniform (flush)	
	deimatic (blanch)	
	passing wave	

tions and photographs on two juvenile specimens studied separately for only a few days. *Metasepia pfefferi* thus revealed an extremely rich repertoire of components. Observations of interacting and sexually mature adults will add still further to the already impressive behavioral repertoire of this species.

Traditionally, most authors have stated that the species *Sepia pfefferi* and its congener from Japanese waters, *S. tullbergi* Appellof (1886), belong in the subgenus *Metasepia* erected by Hoyle (1885b) to contain *pfefferi* (e.g. Adam & Rees, 1966; Adam, 1979; Natsukari, 1979; Lu & Phillips, 1985). However, some authors, such as Iredale (1954), Okutani (1973) and Okutani & Habe (1975) have interpreted *Metasepia* as a genus. The primary characters that distinguish *Metasepia* from *Sepia* are: (1) the short, round, dorsoventrally thickened body; (2) the very unusual morphology of the cuttlebone that is rhomboidal in shape, very broad, covered dorsally with a chitinous layer, and lacks the posterior spine and a dorsal midline rib and



FIGS. 61–68. *Sepia papuensis*, dorsal and right lateral views. Fig. 61. Bipod posture; arms splayed; dark mottle on dorsal mantle and light mottle on ventral mantle. Fig. 62. Bipod posture; mantle, head and fin light components and dark fields prominent. Fig. 63. Tripod posture; dark mottle on dorsal and ventral mantle. Fig. 64. Dorsal view; light uniform, cryptic coloration; dorsal mantle dark spot slightly expressed on right side. Fig. 65. Light mottle; dorsal light components expressed. Fig. 66. Dark mottle, dorsal mantle white components expressed prominently; dorsal head white patches moderately expressed. Figs. 67–68. Two views of light mottle.

(3) the subspherical shape of the egg capsules.

On the basis of these morphological differences and our observations on the chromatic and textural body components and ambulatory flaps, as well as the behavioral modifications associated with the distinctive body patterning and ambulatory locomotion, we believe that *Metasepia* is correctly referred to as a genus distinct from *Sepia*. Photographs (see Fig. 42) and observations (T. Okutani & Y. Natsukari, personal communication; see also fig. 37b in Packard & Hochberg, 1977) on *M. tullbergi* indicate that it is as striking and colorful as *M. pfefferi*.

Roeleveld & Liltved (1985) described fleshy keels on the ventral surface of the mantle in *Sepia pulchra* and its close relatives *S. robsoni*, *S. faurei*, *S. typica* and *S. dubia*. These keels, together with the swollen undersurfaces of the ventral arms, form a "sole" by which the animal adheres to vertical rock surfaces, presumably by forming a differential in pressure. The two keels appear to extend the entire length of the ventral surface of the mantle, one on each side (see figs. 2 and 12 in Roeleveld & Liltved, 1985). *Sepia officinalis* also is reported to have a ventral sole (Hanlon & Messenger, 1988). Thus the form and the function of the ventral keels in the genus *Sepia* are distinct from those of the ambulatory flaps in the genus *Metasepia*. In *Sepia* they serve to hold the animal stationary, while in *Metasepia* they provide an additional means of locomotion.

7. *Sepia papuensis* Hoyle, 1885

Common name: Papuan cuttlefish. This is named here for Papua New Guinea, the locality of original capture.

A. Synopsis

Diagnosis: Mantle elongate, narrow; mantle length to 110 mm; total length to about 200 mm; surface of dorsal and ventral mantle and dorsal and lateral head covered with small papillae; fin narrow and transparent; swimming membranes of arms I, II, and III bear a series of semicircular, elongate lappets; protective membranes of tentacular club separate at base of club in young, fused in adults, the dorsal one much longer; cuttlebone with wide, well-defined mid-dorsal rib and thick chitinous ledge formed by posterior part of fused outer and inner cones; cuttlebone extends anteriorly to between eyes.

Distribution: Central Indo-West Pacific Ocean; Arafura Sea (type locality); Philippines; Bali; Ternate; Australia, from Fremantle, Western Australia, northward around to Queensland (Low Isles). Animals have been captured to about 150 m on sand/silt to mud bottoms.

Life history: Poorly known. To our knowledge, this work represents the first observations on living animals.

References: Hoyle, 1885b; Adam & Rees, 1966; Adam, 1979; Lu & Phillips, 1985.

B. Field observations

A single immature animal (CFER-28) was captured during the day at a depth of 20 m in Watson's Bay. The habitat consisted of flat, open, sand/silt bottom with scattered patches of *Halimeda* sp., *Caulerpa cupressoides* and solitary corals.

The cuttlefish was first observed sitting or resting in the open on the bottom not in association with the *Halimeda*. The surface of the dorsal mantle, head and arms was covered with a light mottled brown and yellow color pattern that closely matched the background color of the sand/silt bottom on which it rested. The animal was captured and placed in an aquarium for observation.

C. Locomotion

During the day the animal often assumed a resting position with the head and the dorsal and lateral arms raised off the bottom, the body supported by the ventral arms and the posterior ventral mantle (tripod posture, Fig. 63). At night the undisturbed animal often was observed floating or hovering motionless in the tank. When floating or hovering, the fins are stationary and folded down against the mantle. Arms I are raised dorsally and arms IV hang down ventrally. When disturbed the animal exhibits a strong escape response and jets away. The arms are flattened and brought together in a cone. When the animal slows down it swims around the tank until it once again begins to float or hover, or it lowers the ventral arms to rest on the bottom in a bipod posture (Figs. 32, 33, 61, 62).

D. Components of body patterns

When the animal rests with the head raised and the body supported on the tips of the

elongate ventral arms, all the arms are strongly compressed or flattened and the protective membranes are closed over the suckers. In this position, arms I are raised and the distal ends are tightly coiled. Arms II also may be raised and curved dorsally and medially. Arms III are extended horizontal to the bottom with the distal ends curved medially. Tiny papillae are raised along the aboral ridge (keel) of all arms.

The mantle of *S. papuensis*, unlike *M. pfefferi*, is elongate and pointed posteriorly. The outline of the cuttlebone is clearly visible through the skin of the dorsal mantle. The head is broad and short, and the eyes are prominent. The fins are very narrow, thin and transparent, which enhances the elongate appearance of the mantle. The finline (fin/mantle fusion line) lies in the upper 1/3 to 1/4 of the body, about in line with the lower margin of the eyelid.

The dorsal mantle is rarely smooth, but normally is uniformly covered with widely scattered papillae in two series: (1) A conspicuous series that consists of a pair of large triangular, flattened primary papillae that emerge from the mantle white spots; (2) Just posterior and lateral to the mantle white spots lies a pair of papillate ridges located along the boundary between the white midline stripe and the darker lateral fields. Additionaly, laterally along the junction of the fins and the dorsal mantle is a series of finline papillae, several of which are longer than the rest. Dorsally on the head, two pairs of large papillae are located over the anterior and posterior ends of each eye. Secondary papillae are smaller and more numerous and hence, less conspicuous than the larger but fewer primary papillae. A small rounded papilla occurs in the center of each dorsal eyelid. The dorsal head between the eyes may be textured with tiny papillae. Ventral to the finline, along the lateral mantle, a series of conspicuous white spots is dotted with numerous primary and secondary papillae.

During the morning (0800-0930), when at rest in contact with the light-colored sandy bottom, the animal assumed a uniform light olive color (Fig. 64) or a very pale beige mottled pattern (Figs. 32, 65) or a reticulated pattern of tiny light brown chromatophores. At night (2200–2315) the animal assumed a darker mottled color consisting of a light yellow overall ground color reticulated with dark reddish-brown (Figs. 33, 63). In both cases the primary papillae are raised moderately and colored beige to white. In these chronic patterns the animal typically matches the color, intensity and texture of the substrate and thus blends cryptically into its surroundings.

While at rest a pair of distinct crescent-shaped mantle white spots is visible, one on each side of the dorsal mantle in the midregion of the mantle (Figs. 34, 35, 65–68). Each white or pale yellow spot has a large papilla in the center. Directly posterior to the mantle white spots is a pair of large mantle dark spots (Figs. 34, 35, 64–68). These are the "eye spots" expressed in the deimatic pattern, and often also visible when the animal assumes light mottled or uniform patterns. A broad midline region that extends the length of the dorsal mantle appears more lightly pigmented than the lateral fields. Dorsal to and along each finline lies a series of white spots that may be expanded into a continuous finline white stripe (Figs. 35, 67, 68). The dorsal mantle is densely covered with tiny red-brown chromatophores that, when expanded, effectively screen all the light areas of the mantle (Fig. 63).

Laterally the mantle is yellow with 6 to 10 large white spots ventral to the finline (Figs. 32, 33). The chromatophores on the lateral mantle are larger than on the dorsal mantle and fewer in number. The flattened ventral mantle is pale with a few large, widely scattered brown chromatophores. The dorsal head is predominantly red overlying or intermixed with yellow. Very fine bluish white lines indicate the outline of the curved anterior edge of the cuttlebone under the surface of the mantle (Fig. 64). Dorsally on the head, medial and anterior to the eyes, are irregular white head patches (Figs. 66–68) that are stippled with minute red-brown chromatopheres. The white head patches can be expanded and merged into a single white head bar. When coalesced they have the appearance of a cauliflower. Laterally, a distinct white stripe extends from the finline through the ventral eyelid where it either terminates just anterior to the eye or continues along the aboral edge of arms III (Figs. 33, 62, 63).

At night the broad curved tips of the flattened arms I are white, contrasting vividly with the red of the remainder of the arm. The proximal papillae along the arm keel are red, the middle ones are white against red, and the distal ones are white. Arms II and III are red with tiny white papillae. Arms III also may be entirely white while all the others are red.

Arms IV are small and red with white papillae. The aboral edge of the arm keel of the ventral arms and the oral surface with the protective membranes normally are white. During the day the ventral arms usually are much lighter, showing little red-brown color.

When the animal is undisturbed and hovering off the bottom the dorsal mantle is a uniform pale olive color with a light beige lateral stripe along the finline. When disturbed by prodding, the animal jets or swims away. The now mottled color is darkened or intensified until a uniform dark brownish-red color is shown. The initial pattern is directed unilaterally toward the side approached. The entire animal darkens only when continually prodded or pursued. The mantle dark spots and white spots are expressed maximally and papillae are extended maximally.

E. Discussion

Even though only one immature animal was available for study, a great deal of information was obtained from it, largely because of the availability of the comprehensive manuscript of Hanlon & Messenger (1988) on *S. officinalis,* which provided the foundation for recognizing and delineating the many components of body patterns, texture and posture.

Sepia papuensis has many of the same components as *S. officinalis,* but the details are species-specific. Due to the cross-sectional nature of our study and the immaturity of the single animal observed, it was not possible to formulate a profile of all the potential patterns and chromatic components (Table 7). However, the basic light and dark components observed are similar to those seen in *S. officinalis* (Hanlon & Messenger, 1988).

The cuttlefishes of Australia are poorly known from the standpoint of observations on living animals. A growing inventory of observations and photographs is being accumulated by biologists and diver/naturalists that eventually should allow a species to be identified on the basis of color and patterns. Watson-Russell (1981) provided photographs of live *S. apama, S. mestus* and *S. plangon* that also occur off Lizard Island. Detailed field observations on *S. latimanus*, another species reported from Lizard Island, are presented in Corner & Moore (1980) and later discussed in Moynihan & Rodaniche (1982). Additional photographs of a cuttlefish tentatively identified as *S. latimanus* are presented in Catala (1986). Our observations on *S. papuensis* indicate that this species, in terms of generic patterns, is similar to the other Australian species indicated above.

Undoubtedly every cuttlefish species has its own repertoire of body pattern components, some more, some fewer than *S. officinalis,* depending upon the selective pressures and conditions imposed during evolution. We can expect a number of variations and permutations on the basic plan that Hanlon & Messenger have revealed. Studies such as are reported here represent the coalescence of behavior and systematics in the sense that more basic, broad-based components represent higher level taxa, e.g. genera or families, while the variations and permutations are species level character traits.

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